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Influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial flood plain of the Middle Fork Flathead River

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THE INFLUENCE OF VERTICAL HYDRAULIC EXCHANGE ON HABITAT HETEROGENEITY AND SURFICIAL PRIMARY PRODUCTION ON A LARGE ALLUVIAL FLOOD PLAIN OF THE MIDDLE FORK FLATHEAD RIVER

by

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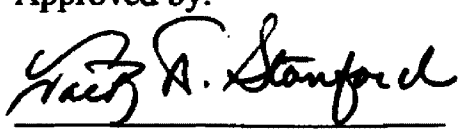

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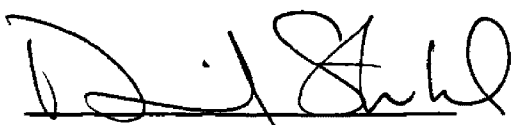

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The effects of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial flood plain of the Middle Fork Flathead River

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Alluvial flood plains are dynamic, heterogeneous mosaics of aquatic and terrestrial habitats which can support high numbers of species and high levels of production. Until recently, surficial processes were thought to structure floodplain ecosystems. However, it now appears that vertical hydraulic exchange between ground and surface waters contributes to the diversity of floodplain habitats and subsequently to overall ecosystem function. Large scale vertical hydraulic exchange was integrated into stream ecosystem theory in the hyporheic corridor concept which stated that water, solutes, and materials move through interstitial pathways determined by floodplain geomorphology, that the convergence of ground and surface waters maintains floodplain heterogeneity, and that these zones of vertical connectivity (ecotones) appear to be hotspots of biodiversity and bioproduction because of the flux of matter from one biophysical state to another.

This study examined aspects of the hyporheic corridor concept, focusing on whether groundwater-surface water ecotones contributed to the heterogeneity of aquatic habitats found on alluvial flood plains, and if this heterogeneity contributed to these ecotones being hotspots of bioproduction. To do this, several different types of groundwater-surface water ecotones (neutral, downwelling, and upwelling in the main channel; and upwelling in floodplain springbrooks) were located throughout the Nyack flood plain of the pristine 5th order Middle Fork Flathead River. Numerous physical and chemical variables and benthic algal biomass were quantified.

Results indicated that vertical hydraulic exchange did in fact contribute to floodplain heterogeneity as physical and chemical conditions varied at different ecotone types. Conditions at main channel sites exhibited high temporal, but little spatial variation, while springbrook sites exhibited high temporal constancy with great spatial variation. Additionally, upwelling ecotones were hotspots of production, generally having significantly more algal biomass as well as higher net accumulation rates than downwelling and neutral sites. This appeared to be due to the upwelling of phosphorus-enriched hyporheic water in a strongly phosphorus-limited system. This is the first study to demonstrate this pattern of algal biomass in a large river and at the floodplain scale.

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Introduction

While traditional stream ecosystem paradigms stressed connectivity, resource gradients, and material fluxes in the longitudinal dimension (Webster and Patten 1979, Vannote et al. 1980, Ward and Stanford 1983), the importance of all three spatial (longitudinal, lateral, and vertical) and the temporal dimensions are now recognized (Ward 1989, 1997). Of particular importance has been the inclusion of the hyporheic zone (i.e., the subsurface region of a stream which is hydrologically established by the advection of channel water; sensu Triska et al. 1989, White 1993) and vertical hydraulic exchange at groundwater-surface water (GW-SW) ecotones, which exist as downwelling (recharge) and upwelling (discharge) variants due to the unidirectional flow of lotic systems (Gibert et al. 1990, Vervier et al. 1992). These ecotones are the linkages between surface and subsurface subsystems. They act as mechanical, photic, and biochemical filters (Vervier et al. 1992); and are sites of high biological activity due to strong physical, chemical, and biological gradients (Edwards 1998, Dahm et al. 1998).

Connectivity between the surface and subsurface is important to both subsystems as well as to overall stream ecosystem function (Grimm and Fisher 1984). Since most groundwater systems depend on organic matter inputs from the surface (Ghiorse and Wilson 1988, Madsen and Ghiorse 1993, Gibert et al. 1994), delivery of organic matter at downwelling ecotones sustains a community composed of heterotrophic bacteria, fungi, and protozoa. Evidence supporting this includes the decrease of organic matter (Vervier and Naiman 1992, Findlay et al. 1993) and microbial cell densities (Ellis et al. in press) along subsurface flowpaths, higher microbial production (Hendricks 1993) and respiration rates (Jones et al. 1995a) at downwelling zones versus upwelling zones, and the positive correlation of microbial activity with quantity and quality of dissolved organic matter (Meyer 1988, Hendricks 1993, Pusch and Schwoerbel 1994, Jones et al. 1995b, Findlay and Sobczak 1996, Craft 1998).

Production by these microbial communities can in turn support complex interstitial food webs (Ellis et al. in press).

Conversely, at upwelling ecotones surface function can be influenced by groundwater discharge (Hynes 1983). Upwelling hyporheic water can be enriched in solutes due to a complex array of biogeochemical processes (Dahm et al. 1998), which include leaching and decaying of organic material, desorption, mineralization, reduction-oxidation, and microbially mediated transformations (Stevenson 1986, Slonsky 1986, Gounot 1994, Fabre et al. 1996). Hyporheic water in a variety of systems has been found to have higher concentrations than surface water for available forms of both nitrogen (e.g., Stanford and Ward 1988, Ford and Naiman 1989, Triska et al. 1989, Valett et al. 1990, Hendricks and White 1991, Wondzell and Swanson 1996) and phosphorus (e.g., Stanford and Ward 1988, Valett et al. 1990, Hendricks and White 1991, Boissier et al. 1996). Since nutrient availability frequently limits benthic algal production, it has been suggested and supported by several studies that nutrient-rich upwelling water can subsidize benthic primary production in streams (Pringle 1987,1990, Stanford and Ward 1988, Stewart 1988, Ward 1989, Coleman and Dahm 1990, Valett et al. 1990, 1994). This enhanced primary production could then in turn support higher secondary production as well.

Vertical hydraulic exchange and subsurface flowpaths can occur at a variety of scales, ranging from centimeters to kilometers (Tóth 1963, Stanford and Ward 1988, Triska et al. 1989, Hill 1990, Bencala 1993, Fetter 1994, Brunke and Gonser 1997, Woessner 1998). Although much work has been done to elucidate the ecological significance of vertical connectivity and exchange (see review in Brunke and Gonser 1997), most of this work has been done at the reach scale (10s of meters; sensu Frissell et al. 1986, Montgomery and Buffington 1998) on low order streams. This small scale (sensu Brunke and Gonser 1997) or local exchange (sensu Tóth 1963, Hill 1990, Fetter

1994) is characterized by short flow paths which are determined by local geomorphologic features such as riffle-pool sequences. Large scale hyporheic flowpaths (sensu Brunke and Gonser 1997) can also exist at the segment scale (100s to 1000s of meters; sensu Frissell et al. 1986, Montgomery and Buffington 1998). This study investigates hyporheic exchange at this larger, segment scale on an alluvial valley of a larger, fifth order river.

Alluvial valley segments (flood plains) are spatially and temporally dynamic heterogeneous mosaics of both aquatic and terrestrial habitats (Pringle et al. 1988, Ward 1998). Until recently, formation of floodplain features (e.g., different channel patterns and types, gravel bars, riparian forests of various ages and successional stages) and ecosystem function were thought to be controlled primarily by surficial events (Patou and Decamps 1985, Junk et al. 1989, Gregory et al. 1991). For example, in northern North America glaciation formed many low gradient, aggraded reaches, which were subsequently reworked by the seasonal inundation and recession of flood waters and the process of cut and fill alluviation.

Stanford and Ward (1993) integrated vertical interactions into the structure and function of large river flood plains in the hyporheic corridor concept. They suggested that water, solutes, and materials move through interstitial pathways determined by floodplain geomorphology, that the convergence of ground and surface waters maintains floodplain heterogeneity, and that these zones of vertical connectivity appear to be hotspots of biodiversity and bioproduction because of the flux of matter from one biophysical state to another. Much of the work done at small scales has supported these main tenets, but this conceptual framework requires further validation at the larger, floodplain scale. This study began to do just that.

This study focused on whether groundwater-surface water ecotones contribute to the heterogeneity found on alluvial flood plains, and if this heterogeneity in turn

contributes to these ecotones being hotspots of bioproduction. To do this, I located several different types of groundwater-surface water ecotones throughout the flood plain, and then examined the influence of vertical hydraulic exchange on physical and chemical conditions and seasonal production of periphyton. I predicted that physical and chemical conditions would vary at different ecotone types, and that higher nutrient levels and higher algal biomass would be found at upwelling ecotones.

Study Site

This study was conducted on the Nyack flood plain of the Middle Fork of the Flathead River, a pristine, oligotrophic river, which forms the southern boundary of Glacier National Park, Montana, USA (Fig. 1). The catchment of the fifth-order Middle Fork Flathead River is approximately 3,000 km^2 in area, ranges from nearly 1,000 m a.s.l. to over 3,000 m a.s.l. in elevation, and is predominantly forested. The basin is dominated by nutrient-poor Precambrian sedimentary and metasedimentary rocks of the Belt Series (mainly argillites) which were uplifted by cordilleran orogeny and subsequently eroded by Pleistocene glaciation and fluvial processes (Ross 1963, Locke 1990, Stanford et al. 1994). Annual discharge is dominated by spring snowmelt, with an average annual discharge of 82.4 m^3/sec and a range from a minimum monthly average of 20.2 m^3/sec in January to a maximum monthly average of 287.5 m^3/sec in June (long term discharge records: 1940-1997; United States Geological Survey, Gauge #12358500, 11 km downstream of Nyack floodplain). The instantaneous peak of record was in May of 1964 and estimated to reach nearly 4,000 m^3/sec.

The Nyack flood plain is a 7-8 km long by 1-2 km wide aggraded alluvial intermountain river segment. It is located 18 km above the confluence of the Middle Fork with the North Fork of the Flathead River, and has an aspect of 333° and an average gradient of 16.1 m/km (Wondzell 1992). The flood plain, a graben-like

depression along the Lewis overthrust fault, is bounded to the up and downstream by narrow bedrock canyons or knickpoints (sensu Stanford and Ward 1993). The alluvial fill is dominated by well sorted cobbles and gravels about 10 m thick, which overlies a low permeability layer of Tertiary clay (Stanford et al. 1994). The active flood plain, which is inundated almost annually, occupies roughly half the width of the valley floor. Channel patterns are braided and anastomosed, creating a complex, dynamic mosaic of aquatic and riparian habitats. Aquatic habitat types include the main channel, side channels, intermittent channels, backwaters, floodplain ponds, groundwater-fed springbrooks, and wetlands. The youngest and most frequently inundated terrestrial surfaces are unvegetated, while progressively older and less frequently inundated riparian areas are dominated by various willows (*Salix spp.*), black cottonwood (*Populus trichocarpa*), and Englemann spruce (*Picea engelmanni*) (Wondzell 1992). These riparian types of Montana are described by Hansen et al. (1988).

Due to well sorted substratum of high hydraulic conductivity (K ranges from 0.1-10 cm/sec, Stanford et al. 1994), the Nyack flood plain has large amounts of interaction between ground and surface waters within an extensive hyporheic zone. The river in the upstream portion of the flood plain is strongly downwelling, losing over 20% of its flow within the first 2 km of the flood plain (Stanford et al. 1994). This water returns to the surface throughout the spatial mosaic of the flood plain: some erupts to form floodplain springbrooks and ponds, while much seems to follow long pathways, returning in a zone of strong upwelling at the downstream end of the flood plain (Stanford et al. 1994). Although specific flowpaths are not known, this upwelling water is thought to be dominated by hyporheic water (i.e., originating from the surface; sensu Triska et al. 1989, White 1993), as the water mass balance which initially described this pattern of exchange did not suggest significant inputs of phreatic water (Stanford, unpubl. data).

Previous studies have characterized conditions within the extensive hyporheic zone on the Nyack flood plain. Well transects and ground penetrating radar (Poole et al. 1997) have revealed highly porous palaeochannels (sensu Stanford and Ward 1993) which appear to be pathways of preferential hyporheic flow. This hyporheic water is highly aerobic with greater than 50% saturation and has higher solute concentrations, including nitrate and soluble reactive phosphorus, than surface water (Stanford et al. 1994, Ellis et al. in press). A diverse interstitial microbial community exists, predominantly attached to sediments (Ellis et al. in press), and respiration rates of this community fall in the middle of the range reported for other systems (Craft 1998). This microbial community appears to support a speciose interstitial invertebrate food web, with over 70 taxa reported thus far (Ward et al. 1994).

Methods

Vertical Hydraulic Exchange

In order to investigate the role of GW-SW interactions on physical and chemical floodplain conditions and surficial primary production, it was first necessary to locate various GW-SW ecotone types, as well as sites of no exchange. Within the main channel, sites were established at the upstream and downstream knickpoints of the flood plain (C1 and C5 respectively, Fig. 2), within the large scale downwelling zone (C2), in a zone of neutral vertical exchange in the center of the flood plain (C3), and within the large scale upwelling zone (C4). Upwelling sites were also established within four floodplain springbrooks (S1-4, Fig. 2), but large downwelling zones were not found for comparison within the springbrooks. S1-2 occurred on the floodplain terrace within ancient meander channels that were blocked at the upstream end by natural deposition of alluvium and woody debris. S3 flowed within an abandoned channel which aerial photos revealed to be the main channel as recently as 1946. S1-3 are occasionally

inundated by surface flow during the hydrograph peak in high water years. S4 was located within an intermittent channel on the active flood plain, was inundated annually, and once river stage receded sufficiently, was fed entirely by hyporheic flow.

In order to locate these sites and quantify the direction and strength of vertical hydraulic exchange, transects of steel piezometers and polyethylene mini-piezometers (Lee and Cherry 1978) were installed to depths of 20-30 cm below the stream bed. Hydraulic heads were measured inside and outside the piezometers and vertical hydraulic gradient (VHG) was calculated as the difference in these hydraulic heads (Δh) divided by the depth of the piezometer (Δl) (see Lee and Cherry 1978, Dahm and Valett 1996). Negative values of VHG represent downwelling, or recharge of the hyporheic zone by surface water, while positive values represent upwelling or discharge of hyporheic water to the surface.

Once areas with the proper hydraulic exchange conditions were located, sites 15 m long and 5 m wide were chosen in straight runs. Main channel sites were established along the river's edge in order to keep depth (<0.4 m) and current velocity (<0.4 m/sec) similar to those found in the springbrooks. Grids of piezometers were installed at each site in August and October 1997.

Statistical comparisons of VHG among the sites were made on log transformed ($\log_{10}(x+4)$) values in order to meet the assumptions of normality and homoscedasticity, and data from both sampling dates were pooled prior to analyses. Using SPSS 7.5 software (SPSS Inc. 1996) for this and all statistical tests, one way analysis of variance (ANOVA) followed by Tukey's (HSD, experimentwise $\alpha<0.05$) test for multiple comparisons were used to compare exchange conditions among sites.

In order to quantify the amount of exchange between ground and surface waters at each site, it was necessary to estimate hydraulic conductivity (K). To obtain a value

for K, Hvorslev slug tests (Hvorslev 1951, Fetter 1994) were performed in each piezometer. At sites with lower K (<0.50 cm/sec), K was calculated using the equation:

$$K = \frac{(\pi)(D)}{(11)(T)} \quad (1)$$

(from Hvorslev 1951) where D (cm) is the diameter of the piezometer and T (sec) is the basic time lag (the time it takes for the water level to fall 37% of the initial change, see Hvorslev 1951, Fetter 1994). For piezometers with higher hydraulic conductivity (>0.50 cm/sec), it was not possible to obtain values of K with this methodology.

When it was possible to estimate values for K, groundwater discharge (Q) was calculated using Darcy's Law:

$$Q = -(K)(A)(VHG) \quad (2)$$

where A (cm^2) is the cross sectional area of the piezometer and VHG is the vertical hydraulic gradient (cm/cm) (Fetter 1994).

Physical and Chemical Conditions

Discharge for the Middle Fork Flathead River was measured continuously 11 km downstream from the Nyack flood plain at a gauging station of the United States Geological Survey (#12358500). Temperature was continuously recorded at each site with thermographs (Hobo®, Onset Computer Corporation) from June-December 1997. Water depth was measured at the location of each rock sampled for algal biomass with a meter stick. Current velocity was measured at the location of each rock sampled for algal biomass using a Price-type mini current meter. Substratum size was assessed at each site using a modified Wolman pebble count (n=100 rocks/site, Rosgen 1996) and d_{50} (the diameter of the intermediate axis at 50% cumulative frequency) calculated. The

gradient of each site was surveyed with an autolevel. Percent open canopy (%CAN) was measured as a surrogate for photosynthetically active radiation using a canopy densiometer.

Surface water grab samples were taken by filling polyethylene bottles within the well-mixed water column at each site monthly during the 1997 study period (April-Dec.) and once in August 1998. Also in August 1998, hyporheic water samples were pumped at upwelling sites from stainless steel piezometers with a Black and Decker Jack Rabbit™ pump. All water samples were placed on ice and returned to the Flathead Lake Biological Station's Freshwater Research Laboratory for analysis. Water samples were analyzed for soluble reactive phosphorus (SRP) and total phosphorus (TP) using a modified automated ascorbic acid method, nitrite and nitrate nitrogen (NO_{2+3}-N) and total persulfate nitrogen (TPN) using the automated cadmium reduction method, dissolved silica (SiO_2) using the automated molybdate-reactive silica method, dissolved organic carbon (DOC) and particulate organic carbon (POC) using persulfate digestion, acid liberation and the infrared CO_2 detection method, and carbonate alkalinity (ALK) using the titration method. All methods can be found in Standard Methods (APHA 1989). Dissolved oxygen (DO), percent oxygen saturation (%SAT), pH, specific conductance (COND), and reduction-oxidation potential (redox) were recorded *in situ* using a Hydrolab™ Surveyor III. Bioavailable atomic N:P ratios were computed using NO_{2+3}-N and SRP. NH_3+NH_4 was not included in these analyses or computations, because concentrations of NH_3+NH_4 from previous samples of both surface and hyporheic water from the Middle Fork Flathead River were consistently below detection (1.0 µg/l, unpubl. data).

All physical and chemical data were log transformed ($(\log_{10}(x))$, except pH which was already in log form and %SAT, %CAN, and N:P which were arcsin transformed prior

to statistical analysis in order to approach normality and meet the assumptions of ANOVA. Independent Samples Student t-tests were performed on pooled main channel sites versus pooled springbrook sites from all sampling dates to compare overall physical and chemical conditions at the different site types. Analysis of variance was conducted separately on main channel and springbrook data pooled for each site from all dates in order to investigate spatial variation within site types, and also on main channel and springbrook data pooled for each date from all sites in order to investigate temporal variation within site types. Paired Student t-tests were used to compare sites between years as well as surface and hyporheic water samples .

Benthic Algal Sampling

Following the scour and recession of the hydrograph peak, natural substratum (n=10) from each site were sampled monthly throughout the 1997 growing season (Aug.-Nov.) and then once in September 1998. Cobbles with intermediate axis size (d_b) of 64-128 mm were selected from established grids using random number tables. From each cobble a 2 x 2 cm square of periphyton was scraped, filtered through a glass fiber filter (Gelman Type A/E 47 mm diameter 1 µm pore size), frozen with dry ice, and returned to the Flathead Lake Biological Station. From this first sample chlorophyll *a* (chl) and phaeophytin (phaeo) were measured using the 90% acetone extraction method (Marker et al. 1980, APHA 1989) and a Perkin Elmer 559 UV-Vis Spectrophotometer. Percent chlorophyll *a* (%chl), an indicator of algal senescence, was calculated from chlorophyll *a* and phaeophytin values (%chl = [chl/(chl+phaeo)]*100). Net chlorophyll *a* accumulation rates (k) were calculated by assuming exponential change of chlorophyll and using the formula:

$$k = \frac{\log (x_{t2}+1) - \log (x_{t1}+1)}{t_2 - t_1} \quad (3)$$

where x_{t1} and x_{t2} are mean chlorophyll values for a site at the first (t_1) and second (t_2) sampling dates following the peak of the hydrograph (Uehlinger 1991, Stevenson 1996).

A second 2 x 2 cm area was scraped from each cobble onto a pre-weighed glass fiber filter and frozen for ash free dry mass (AFDM) analysis (APHA 1989), and an autotrophic index (AI = chl/AFDM) was calculated from chlorophyll and AFDM (Lowe and Pan 1996). A third 2 x 2 cm area was scraped from each rock into a scintillation vial and frozen to determine percent nitrogen and carbon using a Fisons Instruments NA1500 Nitrogen/Carbon Elemental Analysis System, and the ratio of nitrogen to carbon (N:C), an indicator of cellular nutrient status, were computed. The remainder of the periphyton on each rock was scraped into a jar and preserved with Lugol's iodine for species identification. In addition, each rock was washed thoroughly into a 125 μm kick net to collect invertebrates which were then identified to the functional level, in order to examine the relationship between primary and secondary production.

Comparisons of chl, phaeo, %chl, AFDM, chl/AFDM, and N:C were made using two factor (date and site) ANOVAs followed by Tukey's (HSD, experimentwise $\alpha<0.05$) tests for multiple comparisons between sites on each sampling date. Chl, phaeo, and AFDM values were log transformed ($\log_{10}(x+1)$) and %chl, chl/AFDM, and N:C were arcsine transformed before analysis in order to meet the assumptions of ANOVA. Comparisons of 1997 and 1998 data were made using Paired Student t-tests (experimentwise $\alpha<0.05$).

Multivariate Analysis

The transformed physical and chemical data collected at all sites during the 1997 algal growing season (Aug.-Nov.) were ordinated with principal component analysis (PCA) in order to investigate the data's variance-covariance structure through a few uncorrelated linear combinations of the original variables (Joliffe 1986, Johnson and Wichern 1992). A Scree test was employed in order to choose the correct number of axes representing variation explained by common factors, not random variation (Jobson 1992). The reduced dimensionality of the data allowed environmental variation to be visualized by plotting the correlations of the variables with the first two extracted PCA axes. Data from all sites were plotted for each date, in order to allow for interpretation of the different sites without the effects of temporal variation in conditions.

Results

Vertical Hydraulic Exchange

Data from piezometers on the flood plain confirmed the large scale pattern of vertical exchange previously described by Stanford et al. (1994), with strong downwelling below the upstream knickpoint, a central neutral zone, and a strong upwelling zone in the downstream region of the flood plain (Fig. 3). Additionally, all four springbrooks were strongly upwelling (Fig. 3). Vertical hydraulic gradient varied moderately both spatially and temporally within the sites, with the main channel sites being more variable than the springbrooks (mean CVs 3.81 and 0.66 respectively). The direction of VHG did not change at any sites between dates, but the VHG of all but one upwelling site decreased with time and the stage of the river. Despite this variation, ANOVA performed on data from both dates combined revealed statistically significant differences in VHG among sites ($F_{8,351,0.05}$=89.417, $p<0.001$), and Tukey's (HSD, experimentwise $\alpha<0.05$) test showed the downwelling site (C2) to be statistically

different from all other sites, and three of the upwelling sites (C4, S1, and S3) to be significantly greater than all non-upwelling sites (C1-3).

Hydraulic conductivity calculated from Hvorslev slug tests fell within the range of values for K (0.1-10 cm/sec) previously obtained from pump tests (Stanford et al. 1994). Hydraulic conductivity in the main channel (C1-5) and S4 (intermittent channel) was consistently high, with most of the values (145 out of 160) beyond the range of calculation (K>0.50 cm/sec) for this methodology; as the substratum was so highly permeable that it was impossible to fill the piezometers. Values of K for S1-3 were consistently lower, ranging from 0.15 ± 0.07 cm/sec in S1 to 0.18 ± 0.19 cm/sec in S3. Using minimum values of K (0.50 cm/sec) for piezometers that could not be filled, groundwater discharge within the main channel was calculated. Q ranged from 9.70 x 10^{-7} m^3/sec per m^2 at the upwelling site (C4) to -2.56 x 10^{-7} m^3/sec per m^2 at the downwelling site (C2). Upwelling values in the springbrooks were slightly lower than the minimum estimate for C4, ranging from 1.39 x 10^{-7} m^3/sec per m^2 in S2 to 6.18 x 10^{-7} m^3/sec per m^2 in S3.

Physical and Chemical Conditions

The hydrograph of the Middle Fork varied greatly between the 1997 and 1998 water years (Fig. 4). Total volume of runoff for the 1997 water year was 1.20 x 10^{12} m^3, approaching the maximum recorded runoff of 1.32 x 10^{12} m^3 (long term discharge records: 1940-1997; United States Geological Survey, Gauge #12358500). In contrast, volume for the 1998 water year was below average at only 7.56 x 10^{11} m^3. The peak discharge was much greater in 1997 than in 1998 (886 m^3/sec vs. 325 m^3/sec daily mean). There was also a much longer duration of high water in 1997. In 1998 the Middle Fork only peaked above 300 m^3/sec for four days, while in 1997 the Middle Fork remained above 300 m^3/sec for almost two months.

In both 1997 and 1998, the spring runoff was sufficient to scour the substratum within the main channel clean of algal biomass (unpubl. data, pers. obs.). However, the extended duration of high discharge in 1997 resulted in a later recolonization period and shorter growing season. In 1997, depths and current velocities were high enough to inhibit algal colonization and growth through mid-July, while in 1998, algal colonization was apparent by mid-June. Additionally in 1997, the river inundated much of the flood plain, including all of the springbrook sites. Surface runoff flowed through all of the springbrooks, scouring the substratum clean of algal growth in S2 and S4. In 1998, only S4 was inundated and scoured by surface runoff.

The thermal regimes at the different site types varied (Fig. 5). Mean temperature during the 1997 study period (June-Dec.) was significantly higher in the main channel than in the springbrooks (10.15 vs. 7.92°C, Student t-test, $t_{33,0.05}$=2.741, p=0.01, Table 1). When these temperature data were examined seasonally, it was apparent that the springbrooks were significantly cooler than the main channel during the summer (7.95 vs. 10.58°C, $t_{33,0.05}$=3.567, p=0.007, Table 1), but warmer during the fall (4.71 vs. 3.43°C, Table 1). Hence, the springbrooks can be characterized as summer-cool, winter-warm (Fig. 5). The mean temperature range found within the springbrooks was also less extreme than that of the main channel, ranging from 2.1 to 12.4°C in the springbrooks vs. 0.94 to 16.8°C in the main channel (Table 1).

Within the main channel, summer temperatures tended to warm after the river entered the flood plain to maximum temperatures at the neutral site in the center of the flood plain (C3), and then cooled (by as much as 1-2°C on occasion) within the upwelling region (C4) to the coolest temperatures at the downstream knickpoint (C5, Table 1). In contrast, fall temperatures were warmer at the downstream end of the flood plain versus the upstream end. During a cold spell in mid-November anchor ice formed at sites at the

top of the flood plain (C1 and C2, Table 1), but none occurred within the upwelling zone at the bottom of the flood plain (C4 and C5). Also during the cold spell in November, two of the springbrooks (S1 and S2) froze. By that time of the year the stage of the river had decreased so greatly that there was very little water upwelling at the locations of the temperature loggers. Both springbrooks ceased to flow about two weeks prior to the cold period.

During the 1997 study period, other physical conditions also varied between the main channel sites and springbrooks. For pooled data from all dates, depth was significantly higher in the main channel versus the springbrooks (0.20 vs. 0.16 m, Student t-test, $t_{358,0.05}$=3.763, p<0.001, Table 2), as were current velocity (0.29 vs. 0.06 m/s, $t_{358,0.05}$=15.566, p<0.001, Table 2) and percent open canopy (100.00 vs. 59.57, $t_{7,0.05}$=3.364, p=0.012, Table 2). Interestingly, despite the higher current velocity in the main channel, there was no significant difference in the substratum size (d_{50}, Table 2), although main channel sites had a greater representation of larger particles (Fig. 6). Despite high variation, there were significantly higher grazer densities in the springbrooks (7952 vs. 2279 #/m^2, $t_{34,0.05}$, p=0.013, Table 2).

Chemical conditions at the different site types varied as well. Main channel sites had significantly higher average values for pH (8.31 vs. 8.11, $t_{41,0.05}$=4.551, p<0.001, Table 2), dissolved oxygen (9.94 vs. 6.68 mg/l-O, $t_{41,0.05}$=6.920, p<0.001, Table 2), and percent oxygen saturation (96.15 vs. 63.26, $t_{41,0.05}$=10.223, p<0.001, Table 2). These high levels are typical of highly aerated turbulent surface water. Springbrook sites had significantly higher average values for specific conductance (215.19 vs. 164.55 µS/cm, $t_{56,0.05}$= -4.204, p<0.001, Table 2) and alkalinity (118.94 vs. 90.78 mg /l-$CaCO_3$, $t_{56,0.05}$= -5.012, p<0.001, Table 2). These chemical conditions are characteristic of groundwater, as contact with the substratum during subsurface residence results in more ions dissolving into solution.

Some differences in nutrient concentrations between site types were observed. Significantly more silica occurred in the springbrooks (5.79 vs. 4.71 mg/l-SiO_2, $t_{56,0.05}$= -4.830, $p<0.001$, Table 2), again indicating subsurface residence and contact with sediments. There was no significant difference between main channel and springbrook sites for dissolved organic carbon, but there was significantly more particulate organic carbon in the main channel (0.08 vs. 0.06 mg/l-C, $t_{56,0.05}$=2.979, p=0.04, Table 2). Higher levels of POC in the main channel are indicative of delivery of organic material from the catchment, and lower levels in the springbrooks suggest the filtering capacity of sediments as well as utilization by heterotrophic micro-organisms in the hyporheic zone. Some variation in nitrogen was observed, with a significantly higher average for NO_{2+3}-N found in the main channel (39.13 vs. 34.26 µg/l-N, $t_{56,0.05}$=2.183, p=0.03, Table 2). Total persulfate nitrogen was not significantly different between site types, however. Soluble reactive phosphorus was significantly greater in the springbrooks (1.59 vs. 0.82 µg/l-P, $t_{56,0.05}$= -3.952, $p<0.001$, Table 2), but differences for total phosphorus were not significant. Mean values of N:P from all sites were well above the optimal atomic ratio of 16:1 reported by Redfield (1958). Since values higher than 16:1 usually indicate phosphorus limitation of primary production, and the main channel had a significantly higher average values for N:P than the springbrooks (165.6 vs. 78.7, $t_{65,0.05}$= -2.587, p=0.012, Table 2), it appeared that the main channel was more strongly phosphorus limited than the springbrooks.

Within site types, there was a difference in spatial variability of conditions between the main channel sites and springbrook sites. One way ANOVA performed separately on main channel and springbrooks sites for pooled dates revealed few differences among main channel sites, with only depth, current velocity, and grazer density being statistically significant (Table 3). There tended to be higher densities of

grazers at the downstream end of the flood plain (Table 3). In the springbrooks, however, there were large differences in conditions among sites. Analysis of variance revealed statistically significant differences for depth, current velocity, pH, specific conductance, alkalinity, dissolved oxygen, percent oxygen saturation, NO_{2+3}-N, and grazers (Table 4).

Conditions also varied temporally throughout the flood plain. Much greater temporal variation was found within the main channel, as ANOVA on pooled main channel sites demonstrated significant differences among dates for all physical and chemical variables other than grazer density (Table 5). In contrast, the springbrooks represented more constant environmental conditions. There were significant differences only for dissolved organic carbon, redox, silica, soluble reactive phosphorus, total phosphorus, and total persulfate nitrogen (Table 6).

The dynamic temporal patterns in chemical composition within the main channel were very apparent in the NO_{2+3}-N and SRP data. Concentrations of NO_{2+3}-N were highest during spring base flow when groundwater made up the largest proportion of discharge, decreased with dilution by the runoff of surface waters, and then increased again as the river stage decreased (Figs. 7 and 8). Concentrations of NO_{2+3}-N were not as great on the descending limb of the hydrograph as they had been at the same discharge on the ascending limb. This temporal pattern of clockwise hysteresis was also demonstrated by total persulfate nitrogen, N:P, and SiO_2. Specific conductance and alkalinity simply decreased with discharge. On the other hand, SRP exhibited the reverse pattern; concentrations increased with the pulse of spring runoff, and the highest concentrations were found on the rising limb (Figs. 7 and 8). Concentrations of SRP then declined with the river stage as the transport of SRP from the catchment decreased. This pattern of positive clockwise hysteresis was also exhibited by TP, and to some extent by POC and DOC.

There was also variability within site types between the 1997 and 1998 water years. Paired Student t-tests done separately on pooled main channel and springbrook data compared physical and chemical variables from late August 1997 and 1998. Specific conductance and alkalinity were significantly higher, while redox was significantly lower for both site types in the low water year of 1998 (Table 7), suggesting less dilution by surface water. Within the main channel, there was significantly more NO_{2+3}-N but less TPN in 1998 (Table 7). Despite higher SRP in 1998 at four of five main channel sites, this pattern was not significant. Within the springbrooks, there was significantly greater TP in 1998 (Table 7).

Finally in 1998, comparisons were made between nutrients in surface water and in samples of hyporheic water pumped at the upwelling sites. Although the concentrations of both SRP and TP were higher in hyporheic samples at four out of five upwelling sites in 1998 (Fig. 9), paired t-tests did not reveal significant differences for any chemical variables between the two water types. The lack of significance was perhaps due to the small sample size (n=5).

Benthic Algal Biomass

Analysis of variance revealed that both spatial and temporal effects were statistically significant for all measures of algal biomass except N:C (Table 8). Temporally, algal standing crop increased at all main channel sites and most springbrooks throughout the 1997 growing season. Mean chlorophyll *a* values increased from barely detectable levels, 0.2 mg/m^2, after the scouring flood to as high as 26.8 mg/m^2 in the main channel and 152.3 mg/m^2 in the springbrooks by late summer and fall (Fig. 10). This pattern was also exhibited for other measures of algal biomass (Phaeophytin, % chl, AFDM, and chl/AFDM; Table 9) but not for N:C.

Within all dates, most upwelling sites (C4 and S1-4) had more chlorophyll than neutral (C1 and C3) and downwelling sites (C2, Fig. 10). Within the main channel, the upwelling site (C4) had higher standing crop than the downwelling site (C2) on all sampling dates, and this relationship was statistically significant on the final sampling date of 1997 (16.8 vs. 6.4 mg/m^2, Tukey's HSD, experimentwise $\alpha<0.05$, Fig. 10, Table 9). Other measures of algal biomass exhibited similar patterns: the main channel upwelling site had significantly more phaeophytin than the downwelling site (almost 3x) on the final sampling date (18.7 vs. 6.6 mg/m^2, Tukey's HSD, experimentwise $\alpha<0.05$, Table 9) and significantly more AFDM (over 2x) on the last two sampling dates (10.6 vs. 3.95 g/m^2 and 11.8 vs. 4.58 g/m^2, Tukey's HSD, experimentwise $\alpha<0.05$, Table 9). For main channel sites, there were no significant differences for chl/AFDM values at any date, and very few significant differences for %chl (Table 9). There were some significant differences for N:C within the main channel, but no apparent spatial pattern.

The springbrooks generally had significantly greater standing crop values than all main channel sites. For chlorophyll, S1 and S3, which were not completely scoured during runoff, had significantly greater values than all main channel sites on all sampling dates (Fig. 10, Table 9), and on all dates significantly more chlorophyll than S2 and S4 which had been scoured clean (Table 9). By the final two sampling dates of 1997, chlorophyll values for S4 became significantly greater than all main channel sites except for the upwelling site (C2, Fig. 10, Table 9). S2 had significantly greater chlorophyll than all main channel sites only on the September sampling date (Table 9). Again, chlorophyll patterns were indicative of those exhibited by other algal biomass measures. Significance patterns for phaeophytin and AFDM were nearly the same, while there were fewer differences for %chl and chl/AFDM (Table 9). When there were significant differences for N:C, the springbrooks tended to have lower values (Table 9).

The relationship between algal biomass and vertical hydraulic exchange was also apparent from the bivariate plot of chlorophyll and vertical hydraulic gradient for all cobbles sampled in 1997 (Fig. 11). Chlorophyll and vertical hydraulic gradient were significantly positively correlated (Pearson's $r=0.336$, $p<0.001$). There were no chl values above 2.5 $\mu g/m^2$ at downwelling locations.

There was also a strong relationship between primary and secondary producers. For all cobbles sampled in 1997, chlorophyll and invertebrate grazer density were significantly positively correlated (Pearson's $r = 0.309$, $p<0.001$).

Chlorophyll accumulation rate (k), which can be considered a measure of resilience for periphyton (Grimm and Fisher 1989, Uehlinger 1991), varied both temporally and spatially (Fig. 12). Within the main channel, values for k were highest during September, and tended to be higher in the upwelling region of the flood plain; on all sampling dates k was higher at the upwelling site (C4) than the downwelling site (C2, Fig. 12). The highest accumulation rates were found within the springbrooks, and maximum values occurred earlier in the season, with three out of four in August (S1-3, Fig. 12). S1-3 even had biomass loss during September, when maximum values for k were occurring at the main channel sites. S4 exhibited a pattern similar to the main channel sites, and nearly identical to the upwelling site.

Chlorophyll values from September 1998 exhibited the same spatial patterns as those from 1997 (Figs. 10 and 13), and ANOVA yielded significant differences between sites ($F_{8,80,0.05}=110.30$, $p<0.001$). Within the main channel, chlorophyll at the upwelling site (C4) was significantly greater than all other sites (Tukey's HSD, experimentwise $\alpha<0.05$). The downstream knickpoint (C5) also had high biomass, being significantly greater than all main channel sites other than the upwelling site (Tukey's HSD, experimentwise $\alpha<0.05$). Values for chlorophyll at three of the four springbrooks (S1-3)

were significantly higher than all main channel sites (Tukey's HSD, experimentwise $\alpha<0.05$).

When comparing chlorophyll values for 1997 with 1998, all main channel sites had higher biomass in 1998, with significantly greater values found at both knickpoints (C1: $t_{18}= -7.216$, $p<0.001$; and C5: $t_{18}= -12.025$, $p<0.001$, Fig. 13) as well as the upwelling site (C4: $t_{18}= -14.408$, $p<0.001$, Fig. 13). Between 1997 and 1998, the upwelling (C4) and downstream knickpoint (C5) sites increased greatly, while the downwelling (C2) and neutral (C1 and C3) sites increased little. The springbrook sites varied somewhat between the two years. S1 and S3, which were not scoured clean in 1997 and had the highest levels of algal biomass in that year, had slightly less biomass in 1998. This difference between years was not, however, statistically significant. Both S2 and S4 were scoured clean by the spring flood in 1997, but not in 1998. Both had higher biomass in 1998, but only S2 was substantially higher and statistically significant ($t_{18}= -4.182$, $p=0.001$, Fig. 13).

Multivariate Analysis

PCA described 66.7% of total physical and chemical variability in four principal component axes (Table 10). Plots of the first two principal components revealed a spatial segregation of the main channel and springbrooks sites reflecting differences in physical and chemical conditions (Fig. 14a). On all dates, the springbrooks were in areas characterized by high ALK, SiO_2, COND, SRP, and grazers (Fig. 14b). Springbrook sites were not closely clustered at any date, reflecting the heterogeneity of conditions found at the different sites. On the other hand, the main channel sites were always closely grouped within areas characterized by high NO_{2+3}-N, DO, %SAT, pH, substratum size and open canopy (Fig. 14b). At most sampling dates, subtle differences were reflected between the upwelling and downwelling sites which were the main

channel sites plotted furthest from each other. Of the springbrook sites, S4 (intermittent channel) was the most similar to the main channel sites in its characteristics, while S2 was in always quite different from all other sites with strongly negative values on Axis 1.

Temporal changes in conditions at the different sites were also evident in the plots (Fig. 14). The cluster of main channel sites did not move relative to Axis 1, but on Axis 2 it moved from negative values on the first two dates to neutral and positive values for the last two dates as conditions changed with the recession of spring runoff. Although the locations of the springbrooks sites also varied with time, no regular pattern was apparent.

Discussion

Vertical Hydraulic Exchange

Data from piezometers on the Nyack flood plain confirmed the large scale pattern of vertical hydraulic exchange hypothesized by Stanford and Ward (1993) and preliminarily described by Stanford et al. (1994). When the Middle Fork Flathead River entered the highly permeable, low gradient alluvial segment, much of the river recharged the hyporheic zone in a strong downwelling area. Before the downstream knickpoint of the floodplain, this hyporheic water returned to the surface, both within the main channel and springbrooks, and within concentrated or diffuse patches.

Since the specific flowpaths were unknown, the sources of upwelling groundwater, especially within the terrace springbrooks (S1-2), were uncertain. Since there did not seem to be appreciable phreatic inputs on the flood plain (Stanford, unpubl. data) and all four springbrooks were located in abandoned or intermittent river channels, it seemed that hyporheic water flowing through preferential pathways fed the springbrooks. The lack of knowledge of specific flowpaths did not, however, greatly impact this study, as it was not designed to describe changes in conditions along

hyporheic flowpaths. The ecotone types at all sites were still as described, regardless of the specific flowpaths. This study focused on the differences in conditions found at various types of GW-SW ecotones and the effects of those conditions on surficial production. The specific flowpaths may be of interest in further work examining the variation in conditions due to differing degrees of connectivity with and the residence time of the hyporheic water.

Physical and Chemical Characteristics

Large scale vertical hydraulic exchange did in fact appear to play a role in the structural and functional organization of this large alluvial flood plain by contributing to spatial and temporal heterogeneity. Heterogeneity of the habitat template may influence the structure of biotic communities (Frissell et al. 1986, Pringle et al. 1988, Stanford and Ward 1988) and enhance the ecological complexity of floodplain ecosystems (Amoros and Roux 1988, Ward 1998). Since GW-SW ecotones exhibited a variety of physical and chemical conditions, GW-SW exchange appeared to play a role in the complexity of flood plain habitats, and subsequently of communities and ecosystem processes. These linkages, however, require further study.

Heterogeneity was evident in the many physical and chemical variables recorded throughout the flood plain. Different types and degrees of GW-SW connectivity resulted in different thermal regimes. Since groundwater has a high degree of thermal constancy, remaining near the regional mean annual air temperature, and streams dominated by surface water inputs exhibit large diel and annual fluctuations, groundwater and groundwater-fed springbrooks are cooler in the summer and warmer in the winter than surface water (Ward 1985). This less variable thermal regime has been documented on the Nyack flood plain in previous studies (Case 1995, Cavallo 1997). Since temperature can be an important organizing factor for the ecology, evolution, and

distribution of aquatic poikilotherms (see Vannote and Sweeney 1980, Ward and Stanford 1982, Hall et al. 1992), different thermal regimes contributed to the different invertebrate community (Case 1995) and the higher abundance of fishes (Cavallo 1997) found within springbrooks compared to the main channel. My study confirmed the thermal pattern for additional years, as well as for additional springbrooks.

Thermal effects of vertical hydraulic exchange were also evident within the main channel. Upwelling sites at the bottom of the flood plain exhibited less extreme thermal ranges, apparently due to buffering by large-scale upwelling hyporheic water. Cooler summer temperatures could provide thermal refugia both for fish (Bilby 1984, Beschta et al. 1987) and aquatic invertebrates (Ward and Stanford 1982) in upwelling zones. Conversely, warmer winter temperatures could reduce juvenile fish mortality (Cunjak 1988) and aquatic insect dormancy (Ward and Stanford 1982) associated with cold winter conditions. Warmer winter temperatures in upwelling zones could also prevent the formation of anchor ice, which has been reported to drastically, negatively affect stream life (Maciolek and Needham 1952, Chisholm et al. 1987). In conclusion, the thermal heterogeneity found throughout the flood plain as a result of GW-SW exchange clearly provided a wide range of thermal conditions, thus increasing the probability of species packing (Ward and Stanford 1982) and thereby contributing to biodiversity on large alluvial flood plains like the Nyack.

Of the numerous other differences in physical and chemical conditions found throughout the flood plain, the major distinction was between the main channel and springbrooks. In this study, the main channel exhibited high temporal variation due to the pulse and recession of spring runoff and the associated removal or delivery of materials, but little spatial variation. Although few conditions other than vertical hydraulic gradient differed statistically significantly between main channel sites, PCA did reveal slightly different conditions at the upwelling and downwelling sites. These differences

were perhaps a manifestation of vertical hydraulic exchange, but could not be definitively attributed to such. The lack of significantly different chemical conditions amongst main channel sites could be because analyses were conducted on surface water samples, rather than hyporheic samples pumped from piezometers. Upwelling hyporheic water was mixed with and greatly diluted by surface water, potentially masking differences among sites.

In contrast, although springbrooks can be temporally dynamic (e.g., changing locations with channel avulsions), within the scope of this study the springbrooks exhibited temporally stable but spatially variable conditions. Conditions at each of these springbrooks were distinct supporting the hypothesis that vertical hydraulic exchange contributes to floodplain heterogeneity. These differences could be attributed to a variety of possible causes, including the degree of connectivity with both surface and ground waters, groundwater origin, flowpath, and residence time. S4, for example, which was in an intermittent channel, was highly connected with surface waters. It was annually inundated and scoured, and following disconnection from surface flow, the springhead was only about 50 m from the main channel. The conditions found within S4 were more similar to main channel sites than any of the other springbrooks. These similarities were likely due to high connectivity with surface waters. Moreover, if the hyporheic flowpath were directly below the intermittent channel in which S4 occurred, distance traveled by (≈50 m) and residence time of (possibly a few hours or days) hyporheic water would be short. In contrast, S2 differed greatly from all other sites, both main channel and springbrook. Since S2 ceased to flow early in the study period (Sept.), it appeared to become disconnected from its hyporheic source. Specific conductance and alkalinity values increased greatly with time and pH, oxygen and NO_{2+3}-N decreased greatly with time, supporting this theory. This decrease in connectivity or perhaps a very long hyporheic flowpath and residence time most likely

contributed to the unique conditions found within S2. Regardless of cause, the groundwater-fed springbrooks clearly offered a wide variety of physical and chemical conditions for floodplain organisms.

Of the conditions examined in this study, of greatest interest were the nutrients nitrogen and phosphorus. Numerous studies in other systems (e.g., Ford and Naiman 1989, Triska et al. 1989, Valett et al. 1990, Hendricks and White 1991, Wondzell and Swanson 1996) and even within the Flathead Basin (Stanford and Ward 1988, Ellis et al. in press) have reported higher concentrations of NO_{2+3}-N in hyporheic water, as well as in hyporheic-fed springbrooks (Tockner et al. 1997). Nitrate enrichment can be caused by nitrification fueled by mineralization of organic nitrogen during decomposition (Triska et al. 1989, Grimm et al. 1991, Holmes et al. 1994, Jones et al. 1995a, Wondzell and Swanson 1996), or by leaching and desorption from the shallow rooting zone and soils (Hill 1990, Wondzell and Swanson 1996). However, lower levels of NO_{2+3}-N have also been reported in hyporheic water (Triska et al. 1989, Valett et al. 1996), with NO_{2+3}-N uptake and retention due to both physical storage and biotic transformation (Triska et al. 1989, Munn and Meyer 1990, Mulholland 1992, Valett et al. 1996).

In my study, significantly lower levels of NO_{2+3}-N were consistently found in springbrooks fed by hyporheic water compared to the main channel. This was surprising, because previous work on the Nyack flood plain revealed higher concentrations of NO_{2+3}-N both within springbrooks (Stanford unpubl. data) and the hyporheic zone (Ellis et al. in press). Hyporheic systems have been shown to change from sources to sinks of NO_{2+3}-N as oxygen concentrations decrease during the summer (von Gunten et al. 1991, Claret et al. 1998) and denitrification presumably becomes an important pathway for NO_{2+3}-N uptake. However, since denitrification is inhibited in aerobic environments and the Nyack springbrooks and hyporheic zone are highly oxygenated, denitrification is unlikely unless there are regions of slow flow and anoxia.

A possible explanation for this change in relative NO_{2+3}-N concentrations is the high water year of 1997. The extremely large flood pulse of 1997 could have diluted or flushed much of the water in residence from the hyporheic zone. Subsequently, the water upwelling into springbrooks would not have been subsurface for enough time to accumulate high concentrations of NO_{2+3}-N.

Phosphorus dynamics were also quite interesting. Due to the association of higher SRP levels with the pulse of spring runoff in both the main channel and the springbrooks, it appeared that a major source of phosphorus was transport from the catchment. It also appeared that, as reported in other studies (e.g., Stanford and Ward 1988, Valett et al. 1990, Hendricks and White 1991, Boissier et al. 1996), hyporheic water was enriched in available phosphorus. Enrichment of the hyporheic zone could be due to a variety of processes. First is the recycling and leaching of organic material that accumulated during the fall and winter, when low temperatures limit material processing (Timmons et al. 1970, Fabre et al. 1996). There could also be desorption associated with the infiltration of meltwater through sediments (Slonsky 1986, Mulholland 1992, Guonot 1994, Fabre et al. 1996), as well as mineralization and mobilization by microbial activities (Stevenson 1986, Gounot 1994, Dahm et al. 1998). Additionally, phosphorus is typically more available at lower pH due to dissociation from calcium ions and dissolution of apatite (Mulholland 1992). The hyporheic-fed springbrooks had significantly lower pH than the main channel. Another possibility is metal reduction (Dahm et al. 1998). Metal reduction is, however, associated with anaerobic conditions, which have not yet been encountered within the hyporheic zone of the Nyack flood plain, but are certainly possible in areas of low permeability outside of palaeochannels.

In freshwater, available phosphorus is typically an order of magnitude lower than nitrogen, because phosphorus-containing minerals are highly insoluble and phosphorus is strongly retained by biological and chemical processing (Wetzel 1983, Murphy 1998).

Subsequently, phosphorus is often the limiting nutrient for both primary production and decomposition in streams (Elwood et al. 1981, Munn and Meyer 1990), and for heterotrophic production in shallow alluvial and deeper aquifers (Madsen and Ghiorse 1993). Phosphorus limitation of primary production, which typically occurs for values of N:P above 16:1 (Redfield 1958), is largely due to the geology of the basin (Munn and Meyer 1990), and streams with glacial geology are more likely to be phosphorus limited (Gregory et al. 1987). The low levels of phosphorus and the high N:P ratio throughout the flood plain suggested strong phosphorus limitation of primary production. High N:P ratios and phosphorus limitation have been shown in other studies within the Flathead Basin, both within lakes (Bauman 1988, Stanford and Prescott 1988) and streams (Gangemi 1991). In these conditions of strong phosphorus limitation, enrichment is likely to have an effect on primary production, because when SRP concentrations are below 4 µg/l, as on the Nyack flood plain, even a small increase can cause a large increase in benthic algal biomass (Murphy 1998).

Benthic Algal Biomass

This study suggested that vertical hydraulic exchange affected surficial primary production at the large scale of an alluvial segment of a fifth order river. Algal standing crop was higher in upwelling zones, both within springbrooks and the main channel, and differences were greater as the growing season progressed. This pattern was consistent for the measures of biomass (chl, phaeo, and AFDM), but not for measures of physiological status and nutritional quality (%chl, chl/AFDM, and N/C). These results support the hypothesis that higher nutrient levels found at upwelling ecotones enhance surficial primary production, but do not necessarily increase quality as measured by these indices.

Other studies have shown the effects of nutrient-rich substratum or interstitial water on algal biomass in lakes (Jansson 1980, Hurley 1985, Hansson 1989), streams (Pringle and Bowers 1984, Pringle 1987, 1990, Coleman and Dahm 1990, Valett et al. 1994), and on aquatic macrophytes (Fortner and White 1988). However, these studies have all been at smaller scales, in lower order streams, or in the laboratory. The primary study supporting the subsidization of algal biomass in streams by nutrient-rich hyporheic water (Valett et al. 1994), did so in an ephemeral low order nitrogen-limited desert system. My study on the Nyack flood plain appears to be the first to suggest the subsidization of algal production by enriched hyporheic water at the floodplain scale, in a large river, and in a phosphorus limited system.

My study also reported differences in net accumulation rates of chlorophyll throughout the flood plain. Spatial variation in accumulation was exhibited, as upwelling zones within both the main channel and springbrooks had higher rates. This result is consistent with Valett et al. (1994), who stated that the spatial heterogeneity associated with increased accumulation rates in upwelling zones could contribute to ecosystem resilience and stability. Additionally, there was temporal variation of peak accumulation rates and biomass as the springbrooks peaked earlier than sites within the main channel. This temporal variation also contributed to floodplain heterogeneity and possibly to ecosystem resilience, stability, and biodiversity.

Although the strong correlation between chlorophyll and VHG suggested that vertical hydraulic gradient played an important role in the pattern of algal biomass reported, there are other mechanisms that could help explain the differences. The differences in algal biomass and accumulation between the main channel and the springbrooks could be attributed to the many other differences in conditions found between the site types.

Interestingly, temperature, often a very important environmental variable in freshwaters, did not seem to have an effect on algal biomass. Temperature and algal biomass were not correlated, nor did peak accumulation rates of biomass coincide with peak temperatures in either the main channel or the springbrooks. Previous studies examining the effects of temperature on periphyton growth and production in streams are rare, and yield few generalizations as they present equivocal results (DeNicola 1996). Although studies have shown production and growth rates to be positively correlated with and determined by temperatures within thermal tolerance ranges (e.g., Lamberti and Resh 1983, Bothwell 1988), it appears that temperature is not a major controlling factor when other variables such as light (Phinney and McIntire 1965) or nutrients (Bothwell 1988, DeNicola 1996) are limiting. Given the probability of strong phosphorus limitation of algal growth and the lack of a relationship between temperature and algal biomass and accumulation, it appears that temperature is not a controlling factor of algal production on the Nyack flood plain.

Differences in volume and velocity of flow are perhaps important to algal biomass production and accumulation. High discharge and velocity during the peak of the hydrograph scoured the substrate clean in the main channel and within the springbrooks that were sufficiently inundated by surface flow. The loss of surface connectivity and the rapid flow recession then allowed for the earlier accumulation of greater algal biomass in the springbrooks. However, within the main channel it appeared that vertical hydraulic exchange was important to algal biomass accumulation, as main channel sites had few other significant differences in conditions. The possibility that physical or chemical variables important to algal growth were not included in this study also exists, but seems unlikely due to the extensive suite of variables examined.

The hypothesis that nutrient-enriched hyporheic inputs accounted for the differences in algal biomass at upwelling and downwelling sites was supported by

several factors. First were the high values for N:P found throughout the flood plain. These high values suggested strong phosphorus limitation of primary production. Since higher SRP concentrations were found in water pumped from piezometers, the upwelling of phosphorus-enriched hyporheic water could stimulate primary production. Additionally, several water samples taken at the springhead of S4 (roughly 20 m upstream from the sampling site) revealed rapid attenuation of SRP (presumably due to uptake by the dense algal mat), even within such a short distance. This attenuation was not apparent for NO_{2+3}-N. Next, the pattern of higher biomass at the main channel upwelling site was consistent between years of very different hydrologic conditions. Even during the high water year of 1997, with a short period of colonization and growth and tremendous dilution of hyporheic water by surface water, algal biomass was greater and more resilient at the upwelling site. The low water year of 1998, which represented more optimal growing conditions with a longer growing season and less dilution, revealed more pronounced differences between algal biomass at the upwelling and downwelling sites. Between the two years, the greatest increases in algal biomass were at the upwelling site and the downstream knickpoint, the two sites that would be most greatly affected by upwelling hyporheic water and its dilution during the high water year of 1997.

In such an oligotrophic system as the Flathead, upwelling zones or patches (sensu Pringle et al. 1988) may contribute greatly to overall ecosystem production. Although the system is presumably dominated by allocthonous organic matter inputs, algal production in upwelling sites may contribute a large amount of the autochthonous organic matter in the system. Rough estimates from aerial photos, field observations, unpublished data, and extrapolations of the data within this study indicated that by the end of the growing season within the main channel, upwelling zones may contribute algal biomass (chlorophyll) disproportionate to their aerial extent. Upwelling zones,

which covered about 20% of the main channel, were estimated to account for almost 40% of total algal biomass in the main channel. In contrast, downwelling zones, which covered about 30% of the main channel, accounted for less than 15% of algal biomass. Neutral areas covered about 50% of the main channel and accounted for the remaining 45% of algal biomass.

Upwelling zones within springbrooks potentially accounted for an even more disproportionate amount of algal biomass. Using algal biomass data from the four springbrook sites in this study, these upwelling springbrooks alone could produce algal biomass in excess of three times that found in the entire main channel, despite an aerial extent of less than 50% of the area of the main channel in which algae could grow. Since there are far more off-channel upwelling sites throughout the flood plain than those used in this study and these estimates, this suggests that algal production in off-channel upwelling zones could dominate the algal production found on the whole flood plain. These estimates have profound implications for the importance of these often neglected habitats on overall floodplain ecosystem function.

The high algal biomass found in upwelling zones could influence production at higher trophic levels. Upwelling patches of elevated primary production appeared to support higher secondary production, as there was a significant positive correlation between chlorophyll and invertebrate grazer densities. In a system of such limited primary production, higher biomass and more rapid accumulation of algae could be very important to the growth and survival of invertebrate grazers. Subsequently these high densities of grazers could support higher biomass up through invertebrate and vertebrate predators.

It is possible that the grazers themselves could partially account for the pattern of algal biomass found on the flood plain. Although most studies report declines in algal biomass associated with grazing (see review in Steinman 1996), some report no decline

(e.g., Feminella et al. 1989) or an increase in production associated with grazing pressure (e.g., Lamberti et al. 1989). In both studies strong nutrient limitation, such as encountered on the Nyack, was suggested as a possible reason for the lack of decline in algal biomass with grazing. Feminella et al. (1989) suggested that resource limitation slowed algal growth to the point that grazing effects were undetectable within the time frame of the study, while Lamberti et al. (1989) suggested that grazing increased availability of resources to remaining algae and that there were nutrient inputs via grazer excretion. These mechanisms could be at work within this system, however this study is unable to address this issue. Nevertheless, regardless of the mechanism, there are higher levels of both algae and grazers in upwelling zones, both within the main channel and springbrooks, and this fact alone is important to our understanding of the function of floodplain ecosystems.

This study offers further support for the hypotheses of the hyporheic corridor concept (Stanford and Ward 1993) that groundwater-surface water ecotones contribute to the heterogeneity found on alluvial flood plains, and that these ecotones are hotspots of bioproduction. Hendricks (1993) and Jones et al. (1995a) have demonstrated that the downwelling ecotone can be a hotspot of heterotrophic microbial production. Ellis et al. (in press) reported decreasing cell densities of microbes in the hyporheic zone with distance from the river, adding support for this hypothesis on large alluvial flood plains. Valett et al. (1994) demonstrated that the upwelling ecotone can be a hotspot of algal growth in Sycamore Creek, Arizona. This study confirms these findings, scaling up to an alluvial floodplain segment on a large river, further supporting the validity of some aspects of the hyporheic corridor concept across both systems and scales.

These findings, which contribute to our understanding of the structure and function of large floodplain ecosystems, are important because of the paucity of in-tact, large flood plains and our knowledge of their function. Studies of large floodplain

ecosystems have been lacking for numerous reasons, including the cost and difficulty in working on large river systems (Johnson et al. 1995). Additionally, anthropogenic alterations of flood plains (e.g., channelization, dredging, construction of levees, and flow regulation) have greatly reduced the connectivity of most rivers in Europe and North America from their flood plains, subsequently reducing habitat diversity, eliminating off-channel habitats, and impairing overall floodplain function (Gore and Shields 1995). In fact, some large river flood plains are among the world's most severely degraded ecosystems (Johnson et al. 1995). However, as the value of large flood plains is recognized, public attitudes and management directives move towards the conservation and restoration of floodplain ecosystems. In order to succeed in these endeavors, a more thorough knowledge of the natural function of large floodplain ecosystems is needed. This study adds a bit to our knowledge of these systems, however, there is still much work to do.

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Table 1. Thermal characteristics of all sites and pooled site types on the Nyack flood plain of the Middle Fork Flathead River. Average temperatures (± 1 SE, °C) were computed from continuously recording thermographs during the period 1 June to 1 Dec. 1997. Maximum and minimum temperatures (°C) were instantaneous readings during that time period. Values in bold indicate statistical significance.

Site	Avg. Temp.	Summer Avg.	Fall Avg.	Max.	Min.	Degree Days
C1	10.05 ±2.40	10.49 ±1.95	3.33 ±0.33	16.3	Froze	1589.31
C2	10.37 ±2.54	10.88 ±1.99	3.36 ±0.37	17.1	Froze	1640.68
C3	10.38 ±2.34	10.85 ±1.81	3.56 ±0.56	18.6	1.1	1654.02
C4	10.10 ±2.45	10.66 ±1.80	3.33 ±2.52	16.7	1.6	1610.84
C5	9.88 ±2.19	10.04 ±1.72	3.60 ±2.42	15.2	2.0	1558.90
All C	**10.15 ±2.37**	**10.58 ±1.85**	3.43 ±1.24	16.8±1.2	0.94±0.92	1610.75 ±38.46
S1	6.68 ±0.63	6.96 ±0.25	2.16 ±2.01	10.6	Froze	1047.93
S2	7.25 ±1.00	6.95 ±1.53	2.54 ±2.40	13.7	Froze	1081.64
S3	6.82 ±1.34	5.96 ±1.08	8.47 ±0.23	9.0	4.5	1504.99
S4	11.93 ±1.86	11.93 ±2.24	5.69 ±2.77	16.3	3.7	1735.94
All S	**7.92 ±2.37**	**7.95 ±1.28**	4.71 ±1.85	12.4±3.3	2.1±2.4	1342.63 ±334.67

Table 2. Physical and chemical characteristics (mean ± 1 SE) of pooled main channel and springbrook sites during the period 15 April to 1 Dec. 1997. Number of replicates (*n*) is given in parentheses. Significance values are for Independent Samples Student t-tests comparing conditions between the pooled site types. Variables in bold indicate statistical significance.

Variable	Site Type		Statistical Significance
	Main Channel	Springbrook	
Depth (m)	0.20 ±0.10 (200)	0.16 ±0.09 (160)	p<0.001
Current vel. (m/s)	0.29 ±0.17 (200)	0.06 ±0.12 (160)	p<0.001
Gradient (m/m)	0.03 ±0.02 (5)	0.02 ±0.02 (4)	n.s.
Substrate d_{50} (mm)	59.5 ±4.59 (5)	48.8 ±9.0 (4)	n.s.
Open Canopy (%)	100.0 ±0.0 (5)	59.6 ±24.5 (4)	p=0.012
pH (units)	8.31 ±0.06 (35)	8.11 ±0.22 (23)	p<0.001
COND (µS/cm)	165 ±12 (35)	215 ±33 (23)	p<0.001
REDOX (mv)	353 ±23 (35)	373 ±26 (23)	n.s.
DO (mg/l-O)	9.94 ±0.96 (35)	6.68 ±1.69 (23)	p<0.001
% SAT	96.1 ±2.1 (35)	63.3 ±16.7 (23)	p<0.001
ALK (mg/l-$CaCO_3$)	90.78 ±7.89 (35)	118.94 ±16.90 (23)	p<0.001
DOC (mg/l-C)	1.57 ±0.89 (35)	1.16 ±0.63 (23)	n.s.
POC (mg/l-C)	0.08 ±0.03 (35)	0.06 ±0.05 (23)	p=0.004
SiO_2 (mg/l-SiO_2)	4.71 ±0.34 (35)	5.79 ±0.57 (23)	p<0.001
SRP (µg/l-P)	0.82 ±0.24 (35)	1.59 ±0.63 (23)	p<0.001
TP (µg/l-P)	3.81 ±1.64 (35)	4.13 ±2.55 (23)	n.s.
NO_{2+3}-N (µg/l-N)	39.13 ±10.01 (35)	34.26 ±17.09 (23)	p=0.033
TPN (µg/l-N)	52.10 ±13.23 (35)	46.32 ±11.30 (23)	n.s.
N:P (atomic)	165.62 ±107.2 (35)	78.74 ±91.0 (23)	p=0.012
Grazers (#/m^2)	2,279 ±2,012 (20)	7,952 ±10,276 (16)	p=0.013

Table 3. Physical and chemical characteristics of the main channel sites pooled over the period 15 April – 1 Dec. 1997. Values are mean ± 1 SE from untransformed data. P values are for ANOVA performed on transformed data. Variables in bold have statistically significant differences. Values with similar lowercase letters (read across rows) are not significantly different (Tukey's HSD, $\alpha<0.05$).

Variable	n	Main Channel Sites					Statistical Significance
		C1	C2	C3	C4	C5	
Depth (m)	40	0.15±0.08 a	0.27±0.11 c	0.14±0.06 a	0.23±0.09 bc	0.19±0.10 ab	p<0.001
Current vel. (m/s)	40	0.23±0.14 a	0.25±0.15 a	0.26±0.11 a	0.31±0.16 ab	0.40±0.20 b	p<0.001
Gradient (m/m)	1	0.03	0.01	0.07	0.01	0.01	n.s.
Substrate d_{50} (mm)	1	55.0	60.0	67.5	55.0	60.0	n.s.
Open Canopy (%)	1	100.0	100.0	100.0	100.0	100.0	n.s.
pH (units)	7	8.32±0.01	8.32±0.07	8.32±0.04	8.32±0.04	8.27±0.09	n.s.
COND (µS/cm)	7	166±9.43	170±11.9	159±10.6	164±11.8	163±10.8	n.s.
REDOX (mv)	7	381±18.4	349±16.3	340±17.9	350±20.1	345±14.2	n.s.
DO (mg/l-O)	7	10.17±1.09	10.03±0.96	9.87±0.95	9.77±0.99	9.86±0.78	n.s.
% SAT	7	97.3±3.43	95.7±0.5	97.0±1.5	95.7±2.0	95.1±0.8	n.s.
ALK (mg/l-$CaCO_3$)	7	95.20±8.75	91.28±6.92	88.48±7.98	89.04±6.88	89.88±7.24	n.s.
DOC (mg/l-C)	7	1.18±0.33	1.09±0.30	1.65±0.69	1.86±1.15	2.07±1.13	n.s.
POC (mg/l-C)	7	0.08±0.02	0.08±0.03	0.08±0.02	0.07±0.02	0.09±0.04	n.s.
SiO_2 (mg/l-SiO_2)	7	4.92±0.35	4.81±0.27	4.64±0.43	4.56±0.24	4.64±0.27	n.s.
SRP (µg/l-P)	7	0.75±0.23	0.74±0.22	0.90±0.30	0.85±0.19	0.85±0.23	n.s.
TP (µg/l-P)	7	5.24±1.99	3.83±2.11	3.35±1.19	3.33±0.77	3.30±0.68	n.s.
NO_{2+3}-N (µg/l-N)	7	37.23±9.67	36.37±10.54	41.29±10.07	39.71±10.41	41.05±8.73	n.s.
TPN (µg/l-N)	7	51.06±11.29	45.36±9.91	55.57±13.68	55.80±14.80	52.72±13.65	n.s.
N:P (atomic)	7	160.73±113.6	161.85±109.2	158.22±82.2	163.75±98.5	183.53±149.0	n.s.
Grazers (#/m^2)	4	903±682 ab	545±576 a	5410±1835 c	2547±261 bc	1986±1088 abc	p=0.003

Table 4. Physical and chemical characteristics of the springbrook sites pooled over the period 15 April – 1 Dec. 1997. Values are mean ± 1 SE from untransformed data. P values are for ANOVA performed on transformed data. Variables in bold have statistically significant differences. Values with similar lowercase letters (read across rows) are not significantly different (Tukey's HSD, $\alpha<0.05$).

Variable	n	Springbrook Sites S1	S2	S3	S4	Statistical Significance
Depth (m)	40	0.09 ±0.05 a	0.15 ±0.09 b	0.18 ±0.10 bc	0.21 ±0.08 c	p<0.001
Current vel. (m/s)	40	0.07 ±0.18 b	0.01 ±0.03 a	0.17 ±0.07 c	0.00 ±0.00 a	p<0.001
Gradient (m/m)	1	0.00	0.06	0.02	0.00	n.s.
Substrate d_{50} (mm)	1	60.0	35.0	50.0	50.0	n.s.
Open Canopy (%)	1	37.4	43.4	57.4	100.0	n.s.
pH (units)	4-7	8.13 ±0.07 b	7.86 ±0.08 a	8.14 ±0.08 b	8.38 ±0.23 b	p=0.002
COND (µS/cm)	4-7	203 ±4 a	248 ±13 b	181 ±1 a	228 ±38 ab	p=0.003
REDOX (mv)	4-7	376.50 ±22.35	384.00 ±20.22	375.50 ±29.39	353.00 ±20.86	n.s.
DO (mg/l-O)	4-7	7.59 ±0.73 b	4.49 ±1.07 a	7.84 ±0.54 b	6.84 ±1.54 b	p=0.003
% SAT	4-7	69.1 ±8.4 b	41.4 ±10.9 a	75.3 ±4.9 b	68.4 ±14.5 b	p=0.003
ALK (mg/l-$CaCO_3$)	4-7	116.48 ±2.89 ab	142.80 ±9.37b	100.24 ±5.64 a	115.36 ±2.46 ab	p=0.003
DOC (mg/l-C)	4-7	1.67 ±0.93	1.16 ±0.36	0.75 ±0.15	1.02 ±0.25	n.s.
POC (mg/l-C)	4-7	0.03 ±0.01	0.10 ±0.06	0.02 ±0.01	0.06 ±0.02	n.s.
SiO_2 (mg/l-SiO_2)	4-7	5.46 ±0.35	5.76 ±0.48	5.93 ±0.78	6.11 ±0.34	n.s.
SRP (µg/l-P)	4-7	1.73 ±0.85	1.12 ±0.53	1.85 ±0.37	1.67 ±0.24	n.s.
TP (µg/l-P)	4-7	3.18 ±0.30	6.64 ±3.88	3.33 ±0.80	3.12 ±0.43	n.s.
NO_{2+3}-N (µg/l-N)	4-7	47.59 ±2.06 b	7.77 ±5.57 a	41.49 ±8.12 b	42.16 ±3.79 b	p=0.003
TPN (µg/l-N)	4-7	47.84 ±3.54	42.08 ±11.03	45.41 ±13.16	51.15 ±13.77	n.s.
N:P (atomic)	4-7	78.17 ±35.5	68.24 ±118.6	99.20 ±96.0	60.55 ±25.9	n.s.
Grazers (#/m^2)	4	2478 ±1322 ab	1822 ±1403 a	20955 ±13432 c	6557 ±1271 bc	p=0.001

Table 5. Physical and chemical characteristics of pooled main channel sites throughout the study period (April-Nov. 1997). Values are mean ± 1 SE from untransformed data (n=5). P values are for ANOVA performed on transformed data. Variables in bold have statistically significant differences. Values with similar lowercase letters (read across rows) are not significantly different (Tukey's HSD, α<0.05).

Variable	Main Channel Sites							Statistical Significance
	April	June	July	Aug.	Sept.	Oct.	Nov.	
Depth (m)	-	-	0.29 ±0.08 b	0.17 ±0.10 a	0.14 ±0.07 a	0.18 ±0.07 a	-	p<0.001
Current vel. (m/s)	-	-	0.28 ±0.14 b	0.17 ±0.15 a	0.28 ±0.15 b	0.42 ±0.12 c	-	p<0.001
pH (units)	-	-	8.23 ±0.07 a	8.35 ±0.01 b	8.30 ±0.02 ab	8.35 ±0.01 b	8.32 ±0.03 b	p=0.001
COND (µS/cm)	175 ±8 c	113 ±5 a	149 ±3 b	161 ±5 b	167 ±6 c	178 ±3 c	185 ±6 c	p<0.001
REDOX (mv)	-	-	355 ±13 ab	352 ±19 ab	331 ±17 a	373 ±18 b	414 ±21 c	p=0.001
DO (mg/l-O)	-	-	9.05 ±0.22 a	9.22 ±0.11 a	10.09 ±0.16 b	11.41 ±0.30 c	11.91 ±0.16 d	p<0.001
% SAT	-	-	97.8 ±2.7 b	96.0 ±1.0 ab	94.3 ±1.2 a	96.5 ±1.3 ab	94.1 ±0.8 a	p=0.013
ALK (mg/l-$CaCO_3$)	96.35 ±1.19 d	61.85 ±1.53 a	80.42 ±2.19 b	87.81 ±2.54 c	95.42 ±4.43 d	99.46 ±2.07 d	100.35 ±2.18 d	p<0.001
DOC (mg/l-C)	1.12 ±0.56 ab	2.33 ±0.67 b	1.31 ±0.43 ab	1.64 ±1.17 ab	1.45 ±0.86 ab	1.90 ±0.84 ab	0.70 ±0.11 a	p=0.018
POC (mg/l-C)	0.08 ±0.01 b	0.35 ±0.09 c	0.07 ±0.01 b	0.11 ±0.01 b	0.07 ±0.01 b	0.08 ±0.04 b	0.04 ±0.00 a	p=0.001
SiO_2 (mg/l-SiO_2)	5.67 ±0.23 c	4.18 ±0.22 a	4.35 ±0.11 a	4.50 ±0.22 a	4.98 ±0.14 b	5.03 ±0.19 b	5.09 ±0.24 b	p=0.001
SRP (µg/l-P)	0.67 ±0.18 a	2.17 ±0.18 c	1.07 ±0.10 b	0.64 ±0.17 a	0.83 ±0.12 ab	0.73 ±0.28 ab	0.60 ±0.07 a	p<0.001
TP (µg/l-P)	5.26 ±0.90 bc	30.28 ±5.79 d	3.41 ±0.48 ab	5.86 ±1.37 c	2.62 ±0.24 a	3.34 ±1.62 a	2.48 ±0.47 a	p<0.001
NO_{2+3}-N (µg/l-N)	99.50 ±4.09 f	61.17 ±2.19 d	25.14 ±3.18 a	35.41 ±1.74 b	45.74 ±1.85 c	50.23 ±2.48 c	77.19 ±1.26 e	p<0.001
TPN (µg/l-N)	135.52 ±5.84 e	103.39 ±5.85 d	38.93 ±4.68 a	43.40 ±1.85 a	55.97 ±5.75 b	70.10 ±7.23 c	100.44 ±9.90 d	p<0.001
N:P (atomic)	350.37 ±97.2 a	62.70 ±7.1 c	52.27 ±7.0 c	131.21 ±37.8 b	124.99 ±20.0 b	166.35 ±44.5 ab	286.41 ±34.3 a	p<0.001
Grazers (#/m^2)	-	-	2,492 ±2,999	2,489 ±1,882	2,520 ±1,445	1,612 ±1,111	-	n.s.

Table 6. Physical and chemical characteristics of pooled springbrook sites throughout the study period (April-Nov. 1997). Values are mean ± 1 SE from untransformed data (n=4). P values are for ANOVA performed on transformed data. Variables in bold have statistically significant differences. Values with similar lowercase letters (read across rows) are not significantly different (Tukey's HSD, α<0.05).

Variable	Springbrook Sites							Statistical Significance
	April	June	July	Aug.	Sept.	Oct.	Nov.	
Depth (m)	-	-	0.22 ±0.09 b	0.15 ±0.08 a	0.12 ±0.09 a	0.13 ±0.08 a	-	p<0.001
Current vel. (m/s)	-	-	0.08 ±0.09	0.08 ±0.18	0.05 ±0.08	0.04 ±0.07	-	n.s.
pH (units)	-	-	8.05 ±0.14	8.09 ±0.10	8.14 ±0.34	8.14 ±0.19	8.15 ±0.04	n.s.
COND (µS/cm)	211 ±60	156 ±57	227 ±46	203 ±22	211 ±24	221 ±29	201 ±8	n.s.
REDOX (mv)	-	-	368 ±10 ab	378 ±14 abc	345 ±15 a	401 ±21 bc	421 ±21 c	p=0.001
DO (mg/l-O)	-	-	7.39 ±1.19	6.32 ±1.56	6.38 ±2.05	6.81 ±1.60	7.34 ±1.53	n.s.
% SAT	-	-	70.5 ±11.4	60.7 ±13.4	60.8 ±20.5	62.8 ±17.8	66.0 ±16.4	n.s.
ALK (mg/l-$CaCO_3$)	119.89 ±26.85	84.27 ±26.67	114.24 ±17.05	115.08 ±13.41	121.24 ±16.81	124.04 ±18.66	111.63 ±7.46	n.s.
DOC (mg/l-C)	2.35 ±1.11 b	2.11 ±1.07 b	0.89 ±0.38 ab	1.61 ±0.57 b	1.30 ±0.79 ab	0.76 ±0.09 ab	0.48 ±0.02 a	p=0.004
POC (mg/l-C)	0.03 ±0.02	0.23 ±0.16	0.07 ±0.06	0.04 ±0.02	0.07 ±0.06	0.05 ±0.03	0.04 ±0.04	n.s.
SiO_2 (mg/l-SiO_2)	5.14 ±0.79 ab	4.71 ±0.49 a	5.34 ±0.10 b	5.30 ±0.20 ab	6.10 ±0.17 b	6.33 ±0.62 b	5.74 ±0.38 ab	p=0.003
SRP (µg/l-P)	0.51 ±0.22 a	2.11 ±0.41 b	2.28 ±0.79 b	1.31 ±0.42 b	1.78 ±0.24 b	1.15 ±0.33 ab	1.77 ±0.23 b	p=0.002
TP (µg/l-P)	4.07 ±0.32 ab	15.63 ±9.42 b	6.54 ±4.24 ab	2.54 ±0.27 a	4.56 ±1.88 ab	3.48 ±0.32 a	2.99 ±0.02 a	p=0.007
NO_{2+3}-N (µg/l-N)	76.16 ±32.40	51.01 ±10.41	33.08 ±14.21	32.32 ±13.55	33.30 ±18.01	38.03 ±20.90	67.41 ±8.55	n.s.
TPN (µg/l-N)	112.28 ±25.46 d	70.46 ±15.19 bcd	43.81 ±11.78 ab	37.55 ±7.95 a	45.14 ±1.55 ab	58.16 ±9.48 abc	93.30 ±20.6 cd	p<0.001
N:P (atomic)	331.86 ±4.0	53.70 ±5.3	31.02 ±3.9	52.92 ±19.5	43.68 ±29.9	65.74 ±38.9	85.20 ±14.8	n.s.
Grazers (#/m^2)	-	-	8685 ±6265	13,816 ±17,178	4845 ±4958	4461 ±3658	-	n.s.

Table 7. Physical and chemical characteristics of pooled main channel and springbrook sites taken in late August 1997 and 1998. Values are mean ± 1 SE (n=5 for main channel, n=4 for springbrooks) from untransformed data. P values are for Paired Student t-tests between years on transformed data. Degrees of freedom are 4 for the main channel and 3 for springbrook comparisons. Bold values are significantly different.

	Main Channel		Statistical	Springbrooks		Statistical
Variable	24-Aug. 97	27-Aug. 98	Significance	24-Aug. 97	27-Aug. 98	Significance
pH (units)	**8.35 ±0.02**	**8.25 ±0.03**	p=0.007	**8.10 ±0.11**	8.09 ±0.38	n.s.
COND (µS/cm)	**149 ±12**	**194 ±8**	p<0.001	**189 ±23**	**244 ±48**	p=0.037
REDOX (mv)	**352 ±21**	**315 ±16**	p=0.018	**378 ±16**	**330 ±23**	p=0.019
DO (mg/l-O)	9.22 ±0.12	8.94 ±0.43	n.s.	6.32 ±1.78	6.20 ±2.48	n.s.
% SAT	96.0 ±1.1	95.7 ±3.4	n.s.	60.7 ±15.2	65.0 ±31.9	n.s.
ALK (mg/l-$CaCO_3$)	**87.81 ±2.81**	**107.00 ±1.55**	p<0.001	**115.08 ±15.29**	**133.69 ±21.10**	p=0.004
SRP (µg/l-P)	0.64 ±0.18	0.79 ±0.36	n.s.	1.31 ±0.48	1.10 ±0.34	n.s.
TP (µg/l-P)	5.86 ±1.52	4.42 ±1.19	n.s.	**2.54 ±0.31**	**5.69 ±1.34**	p=0.01
NO_{2+3}-N (µg/l-N)	**35.41 ±1.92**	**47.44 ±6.02**	p=0.004	32.32 ±15.45	42.84 ±38.81	n.s.
TPN (µg/l-N)	**43.40 ±2.05**	**21.87 ±3.10**	p=0.001	37.55 ±9.07	30.44 ±13.56	n.s.
N:P (atomic)	131.21 ±37.8	150.65 ±58.8	n.s.	52.92 ±19.4	74.79 ±59.7	n.s.

Table 8. Results of two factor ANOVA (date x site) for all measures of algal biomass during the four month study period Aug.-Nov. 1997.

Dependent Variable		Sum of Squares	df	Mean Square	*F* Statistic	Sig.
Chl	Date	33.907	3	11.302	96.472	p<0.001
	Site	75.991	8	9.499	81.077	p<0.001
	Date X Site	11.691	24	0.487	4.158	p<0.001
Phaeo	Date	1.866	3	0.622	43.644	p<0.001
	Site	6.114	8	0.764	53.628	p<0.001
	Date X Site	1.163	24	0.0484	3.402	p<0.001
AFDM	Date	15.16	3	5.053	50.132	p<0.001
	Site	61.585	8	7.698	76.371	p<0.001
	Date X Site	7.552	24	0.315	3.122	p<0.001
% chl	Date	3.141	3	1.047	13.34	p<0.001
	Site	10.047	8	1.256	15.999	p<0.001
	Date X Site	7.025	24	0.293	3.729	p<0.001
chl/AFDM	Date	8.32E-05	3	2.77E-05	17.363	p<0.001
	Site	1.97E-04	8	2.46E-05	15.391	p<0.001
	Date X Site	9.42E-05	24	3.92E-06	2.457	p<0.001
N/C	Date	2.61E-04	1	0.212	0.212	n.s.
	Site	0.295	8	29.98	29.98	p<0.001
	Date X Site	0.02984	8	3.037	3.037	p<0.001

Table 9. Comparison of all measures of algal biomass at all sites on all sampling dates. Values are mean ± 1 SE from untransformed data. Values with similar lowercase letters (read down columns) at each date are not significantly different (Tukey's HSD, $\alpha<0.05$). Number of replicates (*n*) is 10 for Chl, Phaeo, AFDM, %chl, and Chl/AFDM. Number of replicates (*n*) ranges from 7-10 for N/C.

		Main Channel					
Sites	Date	Chl (mg/m^2)	Phaeo (mg/m^2)	AFDM (g/m^2)	% chl	Chl/AFDM (%)	N/C
C1	1-Aug 97	0.87 ±0.74 a	4.20 ±0.76 a	1.70 ±0.59 ab	16.23 ±12.90 a	0.065 ±0.078	-
	1-Sept 97	0.69 ±0.45 a	3.50 ±0.91 ab	1.23 ±0.46 ab	17.13 ±11.59 a	0.065 ±0.061 a	-
	1-Oct 97	15.41 ±6.46 ab	10.98 ±1.12 abc	5.28 ±1.96 ab	56.47 ±8.84 ab	0.294 ±0.052 cd	0.190 ±0.049 b
	1-Nov 97	18.89 ±14.07 ab	11.74 ±2.47 ab	5.13 ±2.98 a	55.47 ±15.33 e	0.349 ±0.116 e	0.210 ±0.047 c
C2	1-Aug 97	0.50 ±0.70 a	3.02 ±1.12 a	1.75 ±1.11 ab	11.53 ±14.11 a	0.051 ±0.087	-
	1-Sept 97	1.10 ±0.88 a	4.61 ±0.98 ab	2.10 ±1.70 a	18.14 ±11.26 a	0.050 ±0.028 a	0.107 ±0.116
	1-Oct 97	4.88 ±2.27 a	10.50 ±2.16 abc	3.95 ±1.70 a	30.59 ±7.52 a	0.124 ±0.032 abc	0.188 ±0.043 b
	1-Nov 97	6.38 ±3.39 a	6.55 ±1.92 a	4.58 ±2.00 a	45.74 ±16.94 abc	0.155 ±0.094 abc	0.144 ±0.075 b
C3	1-Aug 97	2.70 ±2.97 a	6.35 ±3.26 a	8.10 ±6.96 cde	28.97 ±33.24 ab	0.071 ±0.124	-
	1-Sept 97	4.99 ±2.95 a	4.60 ±0.64 ab	6.30 ±4.08 c	47.62 ±15.87 b	0.086 ±0.032 a	0.124 ±0.012
	1-Oct 97	9.99 ±4.82 ab	9.79 ±3.10 ab	11.70 ±5.32 bcd	48.50 ±10.49 ab	0.088 ±0.031 ab	0.099 ±0.010 a
	1-Nov 97	12.64 ±5.13 ab	9.86 ±3.35 ab	11.03 ±2.83 b	55.48 ±7.81 ab	0.114 ±0.029 ab	0.093 ±0.018 ab
C4	1-Aug 97	1.04 ±1.03 a	1.09 ±1.88 a	2.03 ±1.67 ab	54.29 ±45.30 b	0.059 ±0.051	-
	1-Sept 97	2.93 ±2.61 a	7.97 ±1.91 b	3.90 ±1.79 abc	23.64 ±10.15 a	0.076 ±0.046 a	0.156 ±0.074
	1-Oct 97	19.66 ±18.23 ab	25.01 ±18.30 c	10.63 ±3.65 bcd	43.86 ±28.45 ab	0.219 ±0.230 abcd	0.083 ±0.019 a
	1-Nov 97	26.78 ±12.86 b	18.70 ±6.78 bc	11.78 ±2.91 b	56.62 ±17.79 abcde	0.219 ±0.087 abcde	0.114 ±0.027 ab
C5	1-Aug 97	0.20 ±0.39 a	1.79 ±2.27 a	0.98 ±0.30 a	30.00 ±48.30 ab	0.025 ±0.043	-
	1-Sept 97	0.59 ±0.63 a	4.17 ±0.87 ab	1.75 ±0.86 abc	12.44 ±11.98 a	0.033 ±0.034 a	-
	1-Oct 97	14.15 ±9.67 ab	8.45 ±7.63 a	5.85 ±1.29 abc	61.36 ±32.15 b	0.254 ±0.206 abcd	0.164 ±0.024 b
	1-Nov 97	10.30 ±4.74 ab	6.27 ±2.70 a	5.18 ±1.70 a	63.49 ±14.43 abcd	0.197 ±0.052 abcd	0.125 ±0.039 ab

Table 9. Continued.

		Springbrooks					
Sites	Date	Chl (mg/m^2)	Phaeo (mg/m^2)	AFDM (g/m^2)	% chl	Chl/AFDM (%)	N/C
S1	8/1/97	53.76 ±52.20 b	31.99 ±24.72 b	21.08 ±16.14 de	55.52 ±28.73 ab	0.248 ±0.310	-
	9/1/97	138.80 ±77.09 c	30.84 ±13.18 d	60.43 ±31.29 d	80.33 ±3.91 c	0.261 ±0.173 bc	0.085 ±0.021
	10/1/97	124.75 ±60.40 c	29.32 ±12.81 d	46.20 ±23.12 e	79.23 ±5.71 b	0.282 ±0.136 bcd	0.077 ±0.014 a
	11/1/97	126.29 ±73.78 c	31.66 ±18.27 d	51.08 ±26.44 c	79.09 ±3.72 cde	0.272 ±0.076 cde	0.071 ±0.005 a
S2	8/1/97	9.95 ±13.28 a	7.53 ±6.29 a	8.95 ±10.45 cd	46.27 ±26.54 ab	0.129 ±0.181	-
	9/1/97	42.37 ±35.31 b	17.24 ±8.68 c	27.93 ±20.75 d	62.60 ±16.67 b	0.158 ±0.109 ab	0.066 ±0.023
	10/1/97	17.18 ±10.46 ab	18.38 ±8.00 bcd	27.48 ±20.94 de	46.32 ±17.11 ab	0.074 ±0.029 a	0.079 ±0.025 a
	11/1/97	27.11 ±25.69 ab	19.00 ±7.87 bcd	27.30 ±19.40 bc	45.66 ±22.17 a	0.095 ±0.109 a	0.093 ±0.040 ab
S3	8/1/97	43.45 ±49.22 b	19.81 ±12.48 b	21.80 ±16.68 e	56.56 ±16.95 ab	0.239 ±0.236	0.078 ±0.049
	9/1/97	152.32 ±191.9 c	25.49 ±13.72 cd	47.40 ±41.27 d	79.64 ±10.02 c	0.386 ±0.236 c	0.125 ±0.042
	10/1/97	82.94 ±62.09 c	25.05 ±11.44 d	26.18 ±16.20 de	72.30 ±9.65 ab	0.336 ±0.214 d	0.084 ±0.018 a
	11/1/97	92.20 ±61.06 c	27.59 ±18.89 cd	29.45 ±19.70 c	73.59 ±8.17 de	0.332 ±0.101 de	0.109 ±0.034 ab
S4	8/1/97	1.57 ±1.39 a	5.94 ±2.27 a	4.55 ±1.83 bc	21.56 ±17.51 ab	0.032 ±0.029	0.062 ±0.094
	9/1/97	5.27 ±3.67 a	3.10 ±0.84 a	5.28 ±3.40 bc	56.98 ±13.84 b	0.108 ±0.069 ab	0.173 ±0.101
	10/1/97	25.07 ±17.06 b	15.38 ±7.70 abcd	14.10 ±11.07 cd	58.12 ±11.55 ab	0.188 ±0.069 abcd	0.102 ±0.045 a
	11/1/97	29.56 ±18.03 b	14.10 ±3.44 abc	12.18 ±6.10 b	60.36 ±20.35 bcde	0.236 ±0.135 bcde	0.086 ±0.023 a

Table 10. Variable correlations within the four PCA axes which explain 66.7% of total variation. Correlation values greater than + or –0.5 are shown in bold type.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
%SAT	**0.960**	-0.0162	0.0516	-0.0430
DO	**0.900**	0.233	0.236	-0.0875
d50	**0.831**	0.246	0.0147	0.0961
%CAN	**0.820**	-0.305	0.0632	0.234
pH	**0.808**	0.158	0.123	0.252
NO_{2+3}-N	**0.678**	**0.627**	0.0945	0.158
Current Vel	**0.620**	0.000387	0.247	-0.339
ALK	**-0.889**	0.0727	0.320	0.123
COND	**-0.822**	0.0603	0.423	0.176
SRP	**-0.696**	-0.462	-0.0197	0.113
SiO_2	**-0.694**	0.392	0.244	0.254
Grazers	-0.0890	**0.523**	-0.447	0.258
POC	0.207	**-0.788**	0.212	0.293
TPN	0.221	0.245	**0.743**	0.302
Redox	-0.460	0.182	0.273	**-0.532**
% Variance	36.9	14.5	9.1	6.2

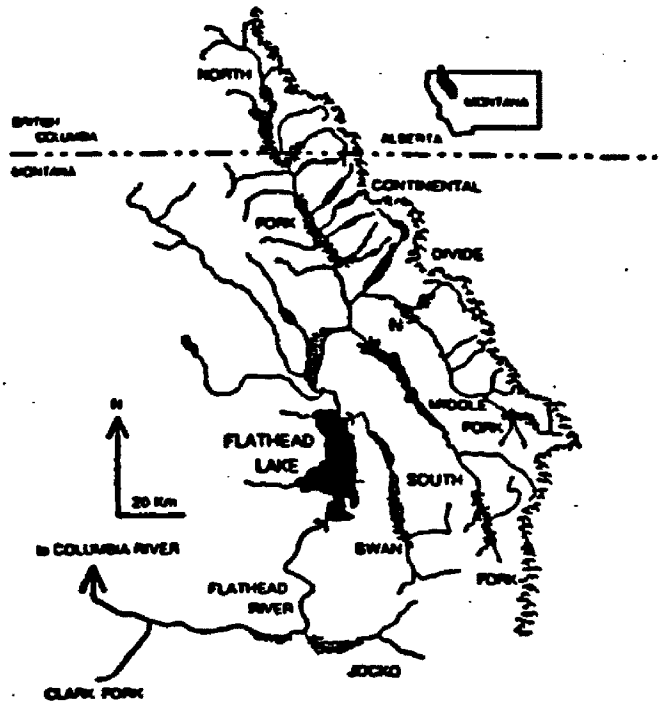

Fig. 1. The location of the Nyack floodplain (N) within the Flathead River catchment in Montana, USA and British Columbia, Canada. The Nyack and other alluvial floodplains within the catchment are stippled (modified from Stanford and Ward 1993).

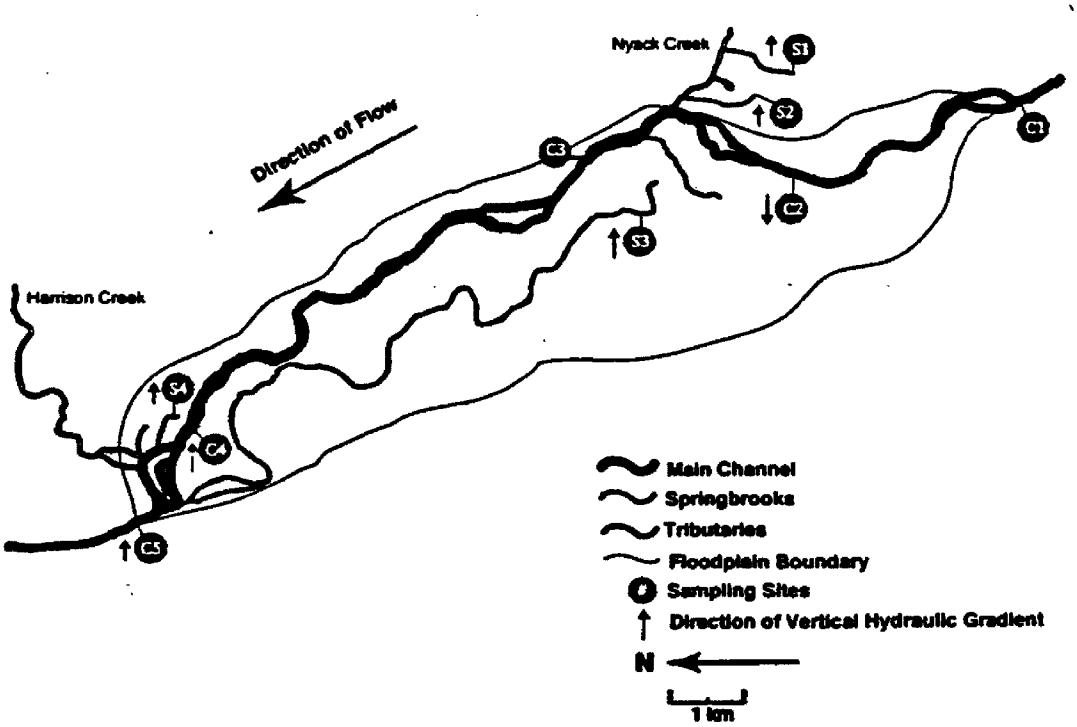

Fig. 2. The Nyack floodplain of the Middle Fork Flathead River. Main channel (C1-5) and springbrook (S1-4) site locations and direction of vertical hydraulic exchange are indicated.

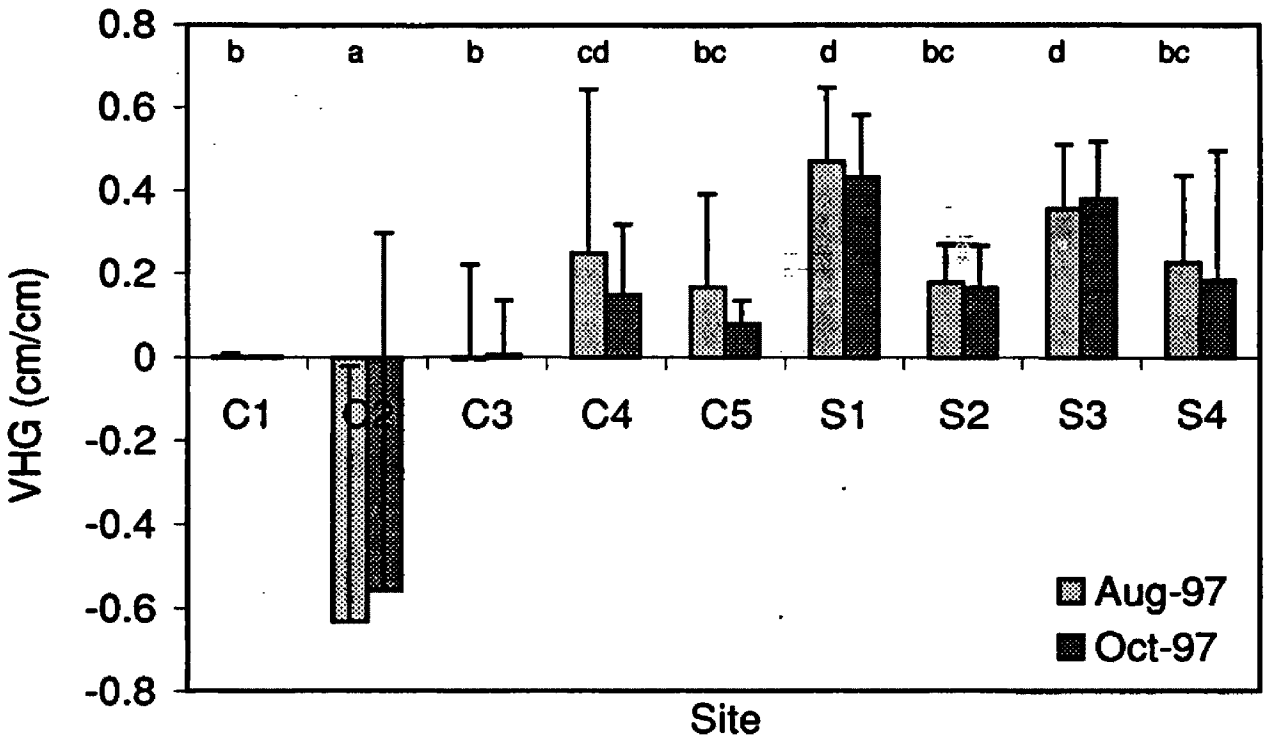

Fig. 3. Untransformed mean (+1 SE) vertical hydraulic gradient from piezometers at all sites on two dates (n=35 on each date for each main channel site C1-5, n=25 on each date for each springbrook site S1-4) See Fig. 2 for locations of sites on the floodplain. Sites with similar lowercase letters are not significantly different (Tukey's HSD, experimentwise $\alpha<0.05$). Statistical analyses were conducted on transformed data.

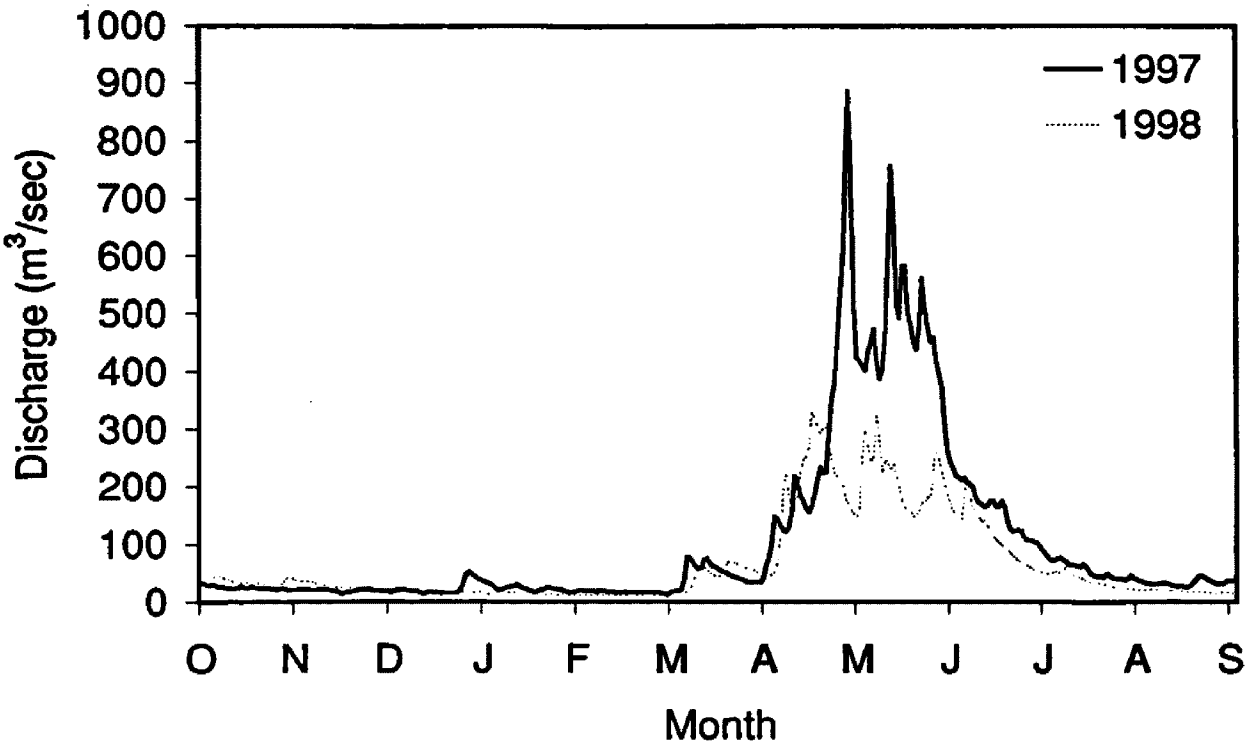

Fig. 4. Average daily discharge of the Middle Fork Flathead River for two years (USGS gauging station #12358500).

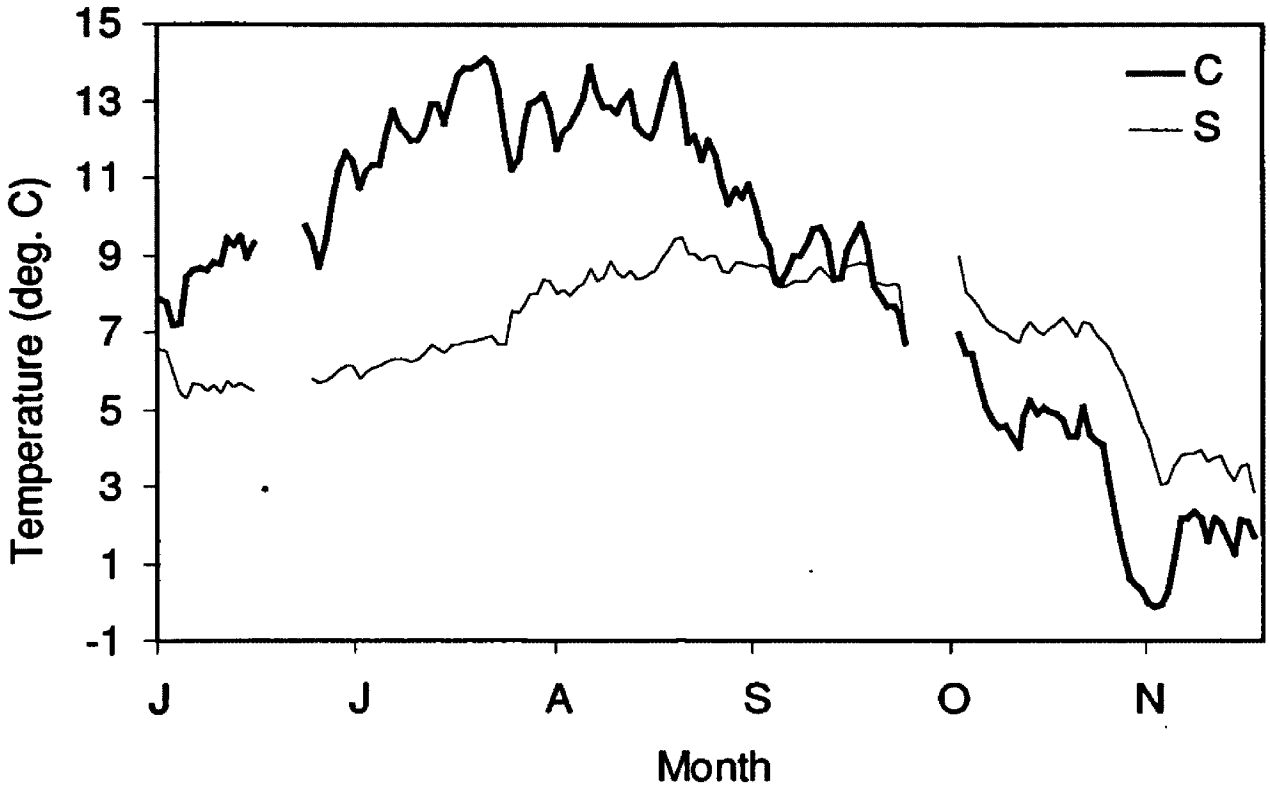

Fig. 5. Average daily temperature on the Nyack floodplain of the Middle Fork Flathead River for pooled main channel (C) and springbrook (S) site types during the 1997 study period.

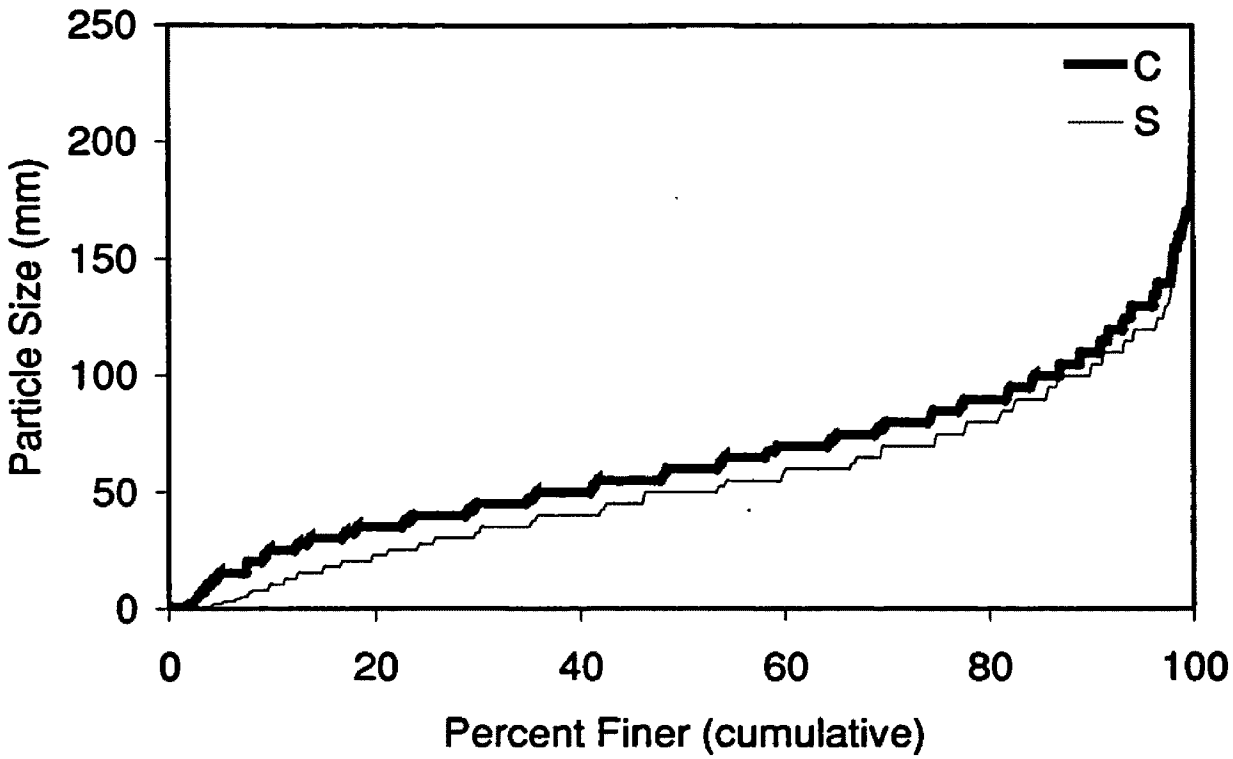

Fig. 6. Substratum particle size distribution for pooled main channel (C) and springbrook (S) site types on the Nyack floodplain of the Middle Fork Flathead River (n=500 for the main channel, n=400 for the springbrooks).

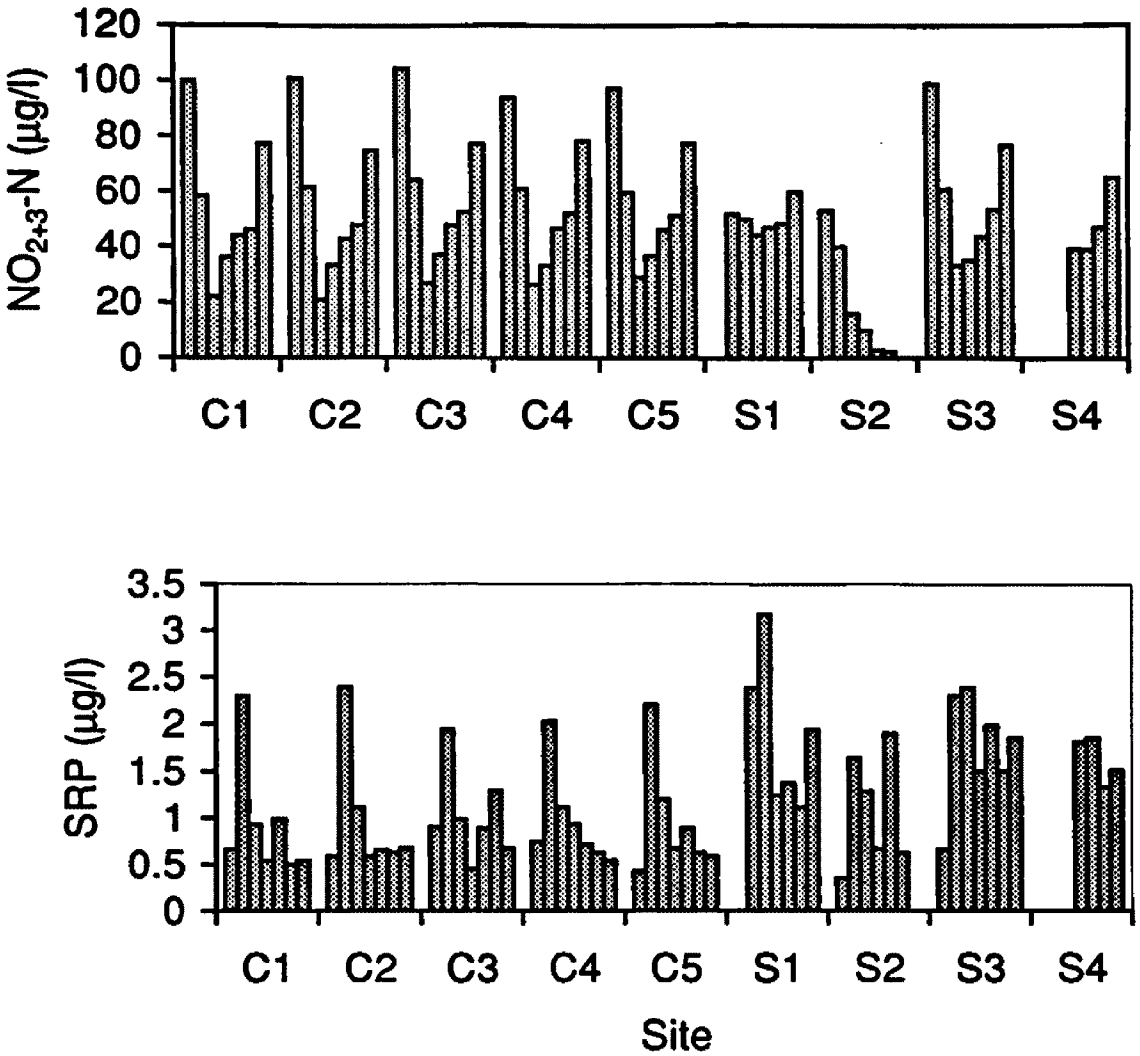

Fig. 7. Nutrient concentrations at all sites on the Nyack Floodplain of the Middle Fork Flathead River. Each cluster of bars represents concentrations at a site over the time period April-November 1997. Each bar represents a single sample.

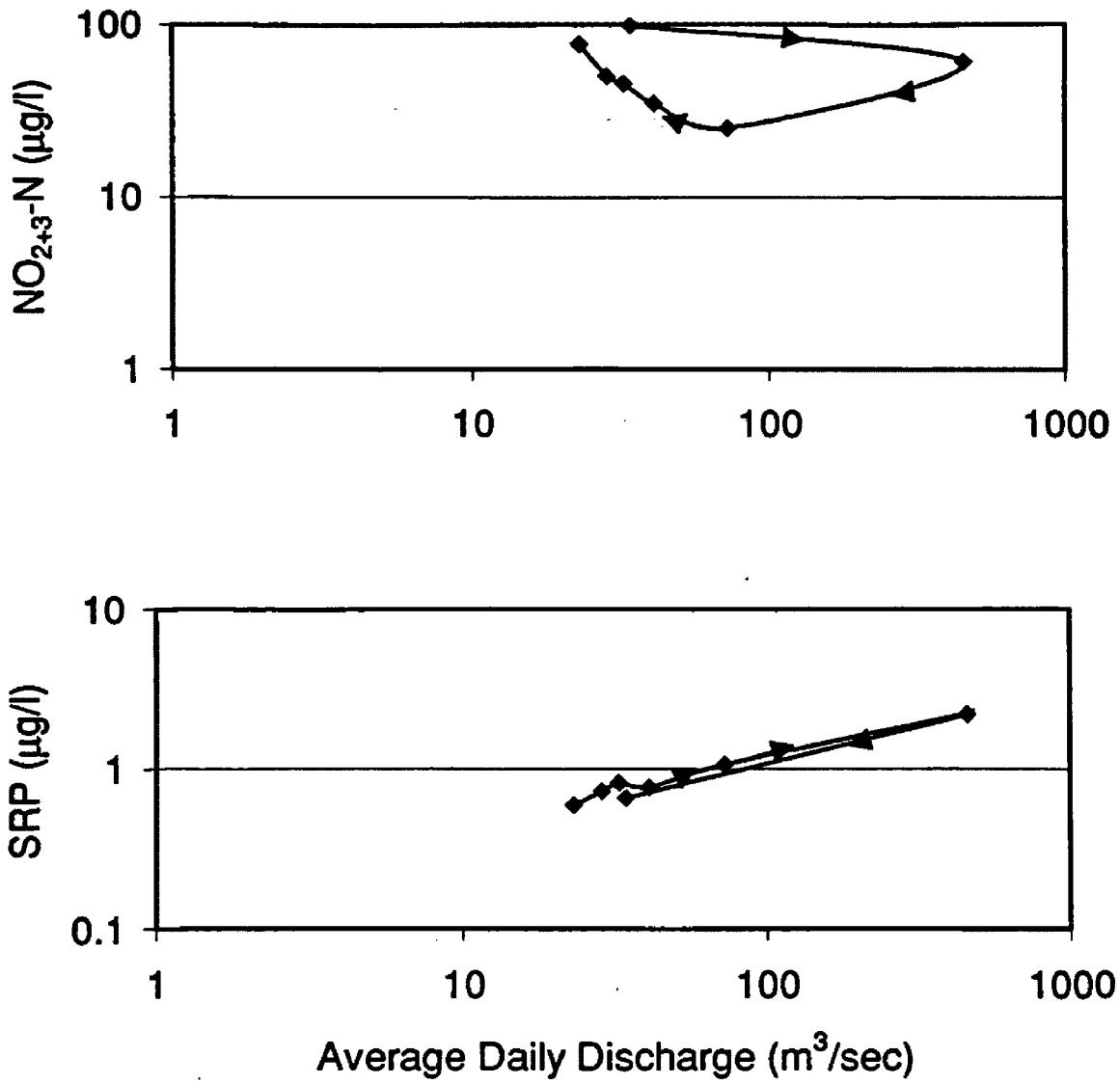

Fig. 8. Hysteresis in discharge-nutrient concentration relationships for pooled main channel sites of the Middle Fork Flathead River on the Nyack floodplain during the period April-November 1997 (*n*=5 for each point).

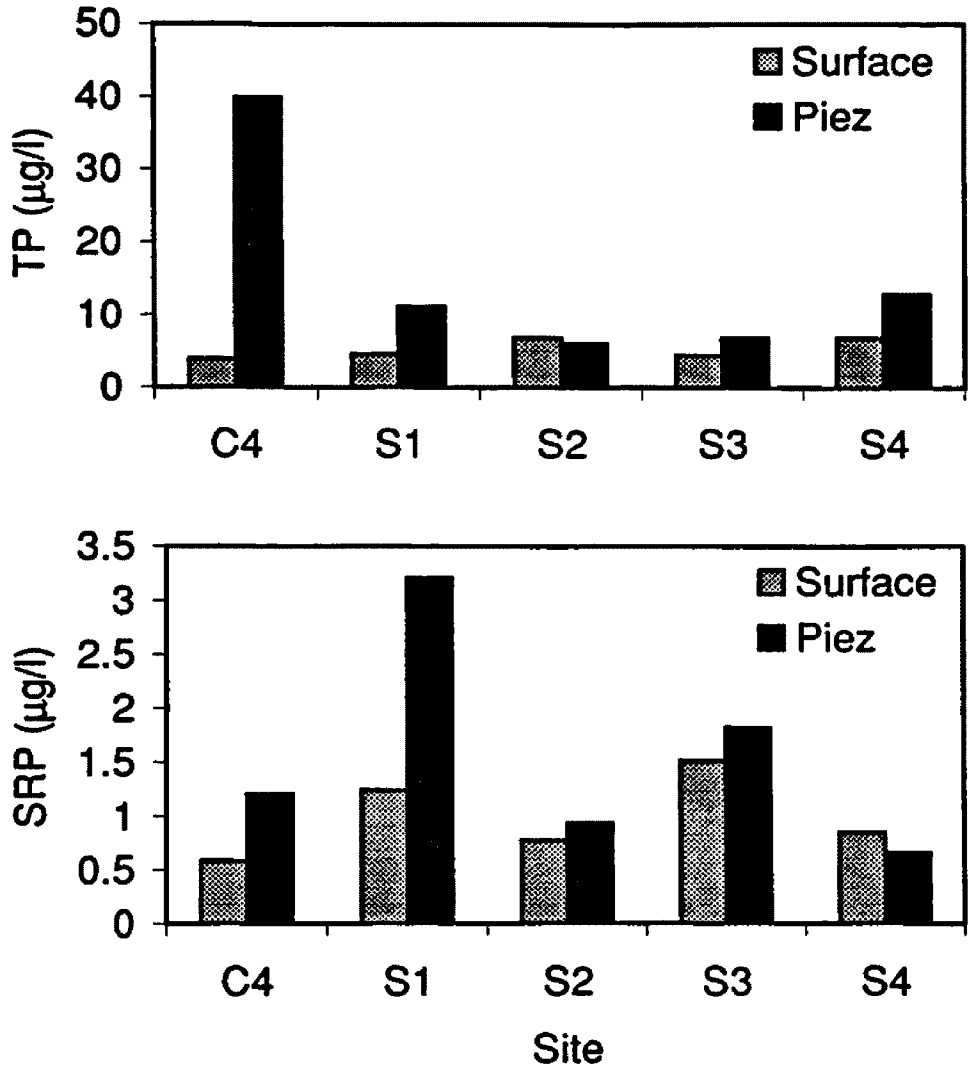

Fig. 9. Phosphorus concentrations in surface and hyporheic water samples taken from piezometers at upwelling sites on the Nyack floodplain of the Middle Fork Flathead River on 27 Aug. 1998. Each bar represents a single sample.

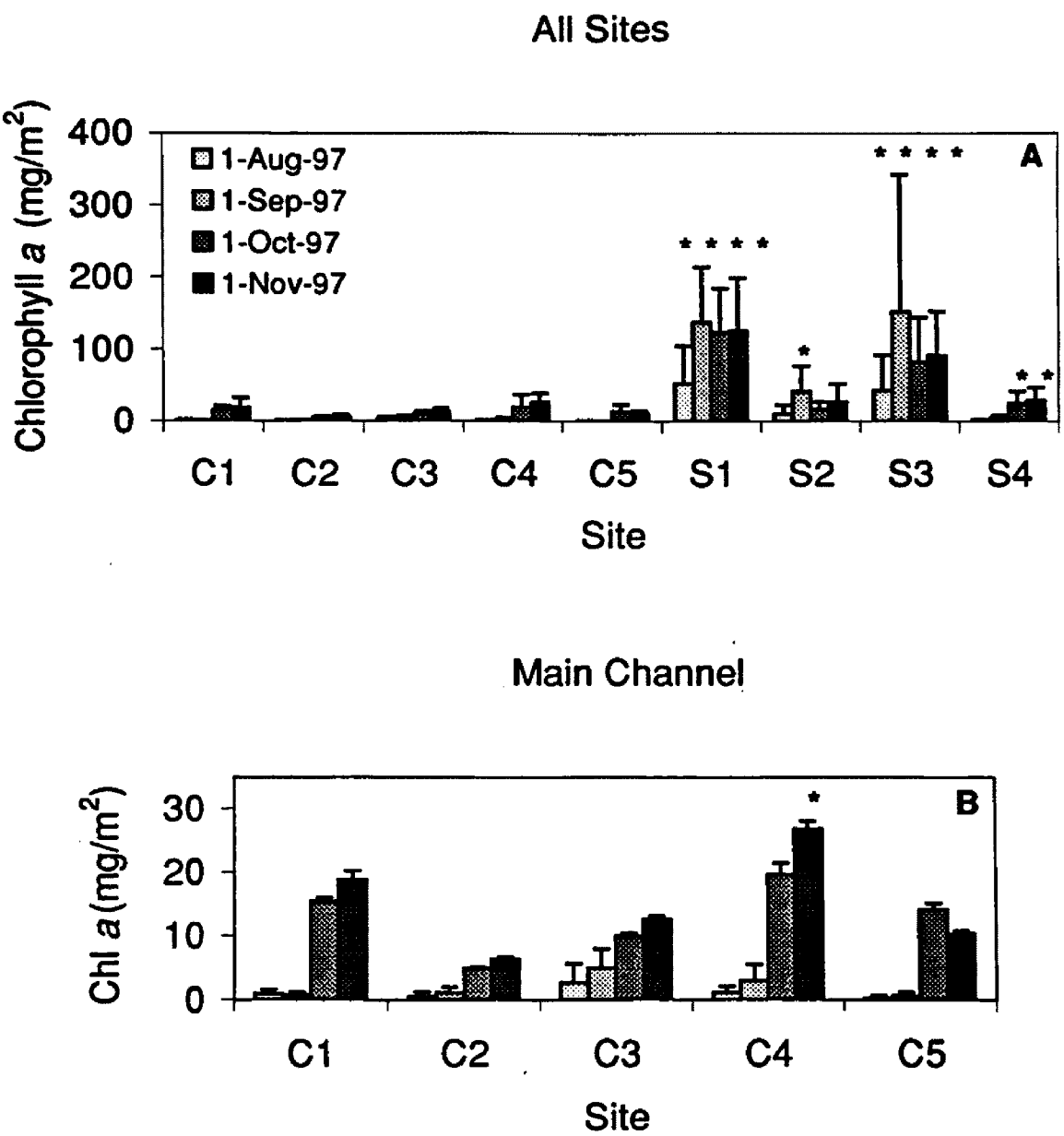

Fig. 10. Mean chlorophyll *a* concentrations (+ 1 SE, n=10) from natural substratum on four dates in 1997 for all sites (A) and for main channel sites (B) on the Nyack floodplain of the Middle Fork Flathead River. In A, * represents significantly greater values on a given date (Tukey's HSD, experimentwise $\alpha<0.05$) than all main channel sites for S1-3, and than all main channel sites other than the upwelling site (C4) for S4. In B, * represents significantly greater values on a given date (Tukey's HSD, experimentwise $\alpha<0.05$) than the downwelling site (C2).

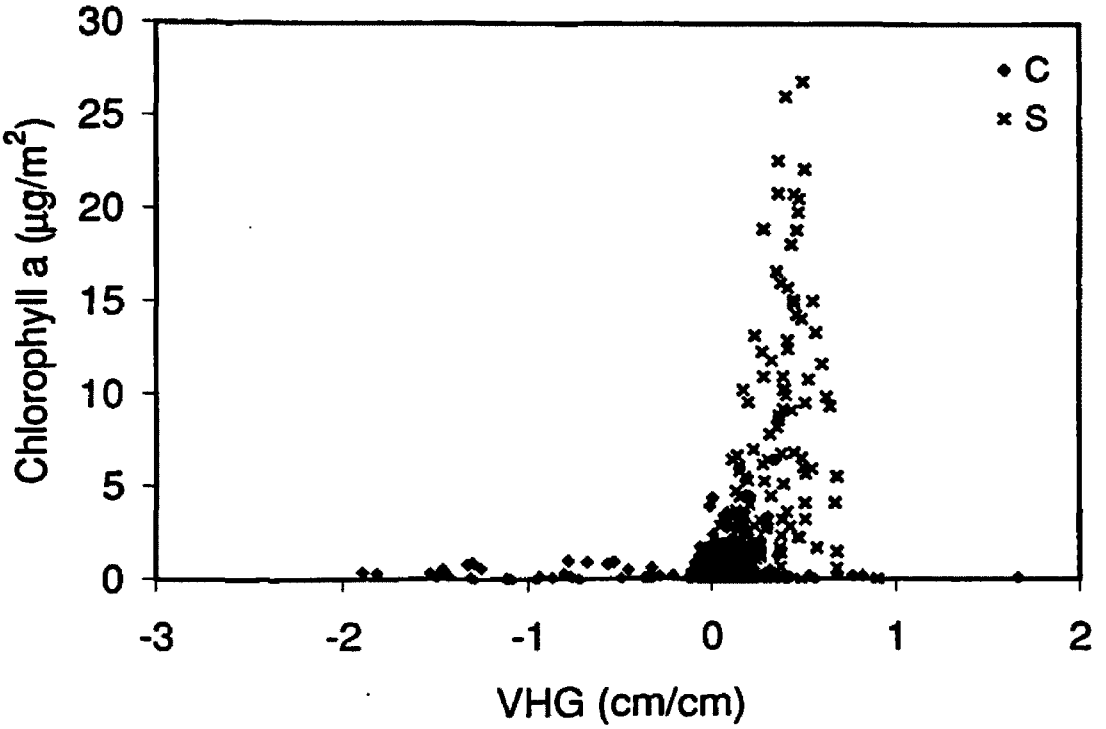

Fig. 11. Chlorophyll *a* vs. vertical hydraulic gradient for all cobbles collected from all sites on all 1997 sampling dates.

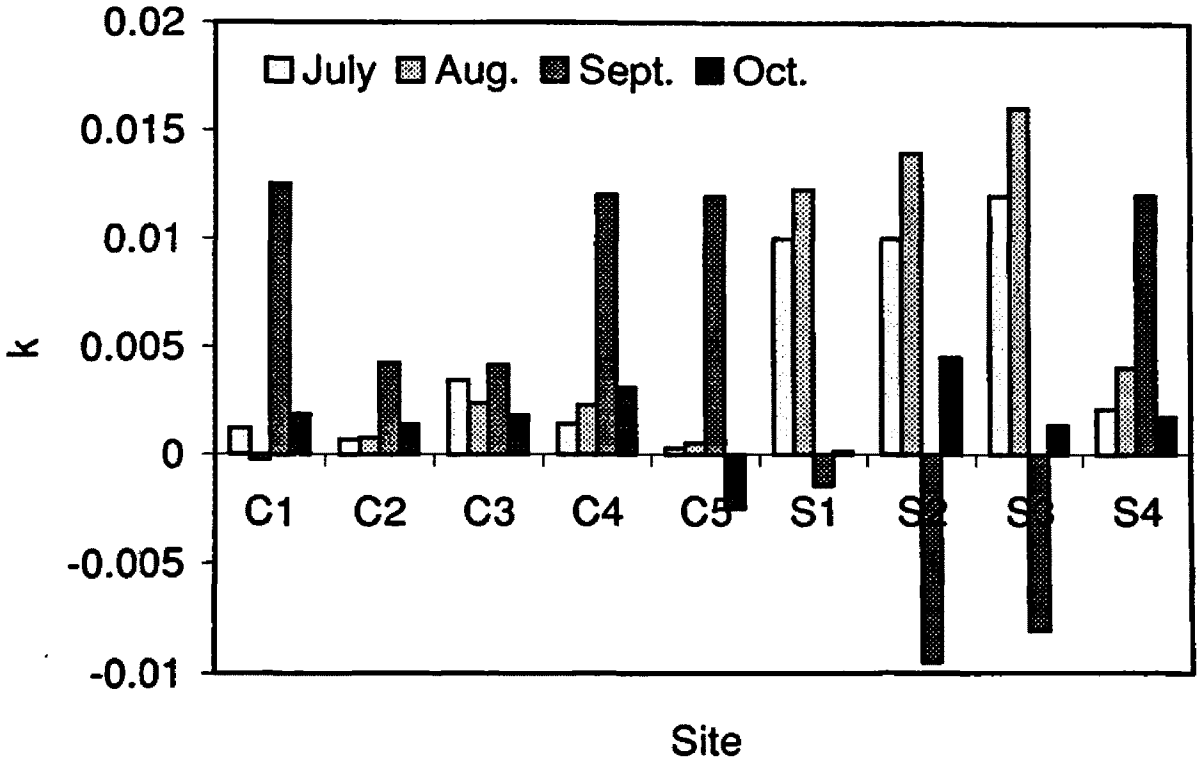

Fig. 12. Net accumulation rates (k) of chlorophyll *a* at all sites during the 1997 growing season.

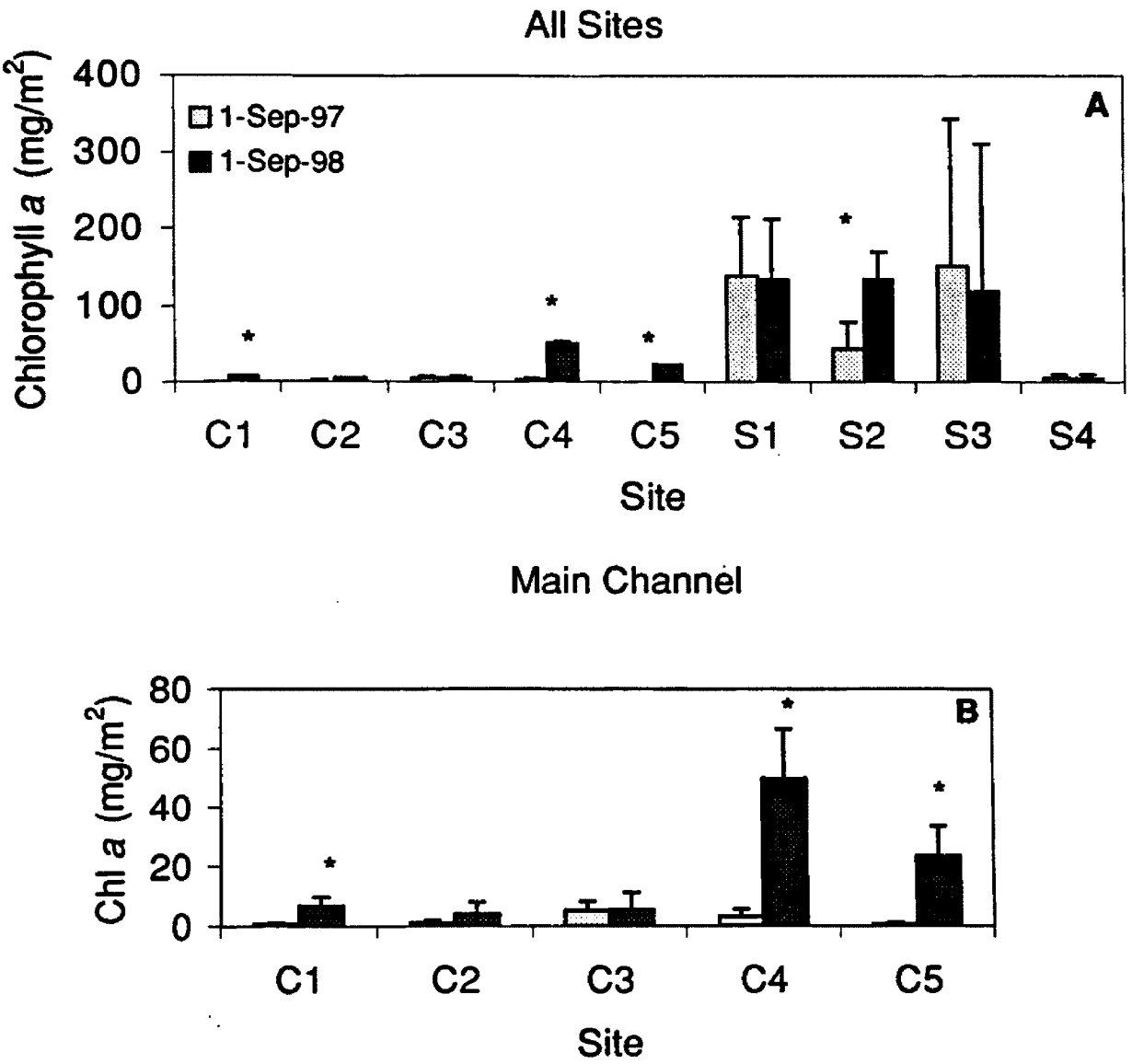

Fig. 13. Mean chlorophyll *a* concentrations (+ 1 SE, *n*=10) from natural substrata on 1 Sept. 1997 and 1998 for all sites (A) and for main channel sites (B) on the Nyack floodplain of the Middle Fork Flathead River. In both A and B, * represents significantly greater values at a particular site in 1998 versus 1997 (Independent Samples Student T-test).

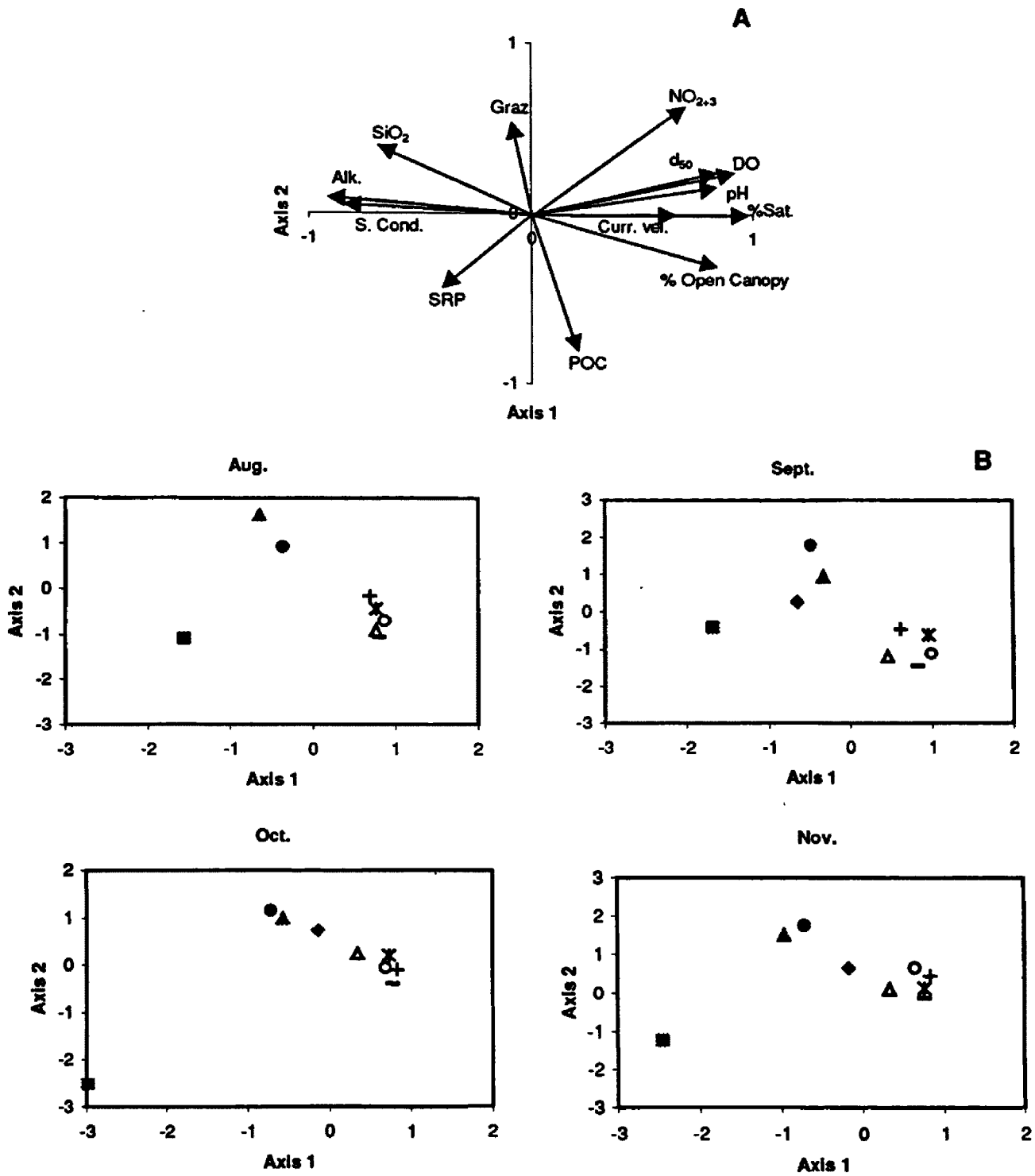

Fig. 14. Graphical interpretation of the principal component analysis. A is a Axis 1-Axis 2 correlation circle. B are Axis 1-Axis 2 factorial maps for each date. Axis 1 explained 36.9% of the total variance, while Axis 2 explained 14.5%. See Table 10 for details on axes. Symbols denote sites: C1 = △, C2 = –, C3 = ○, C4 = +, C5 = *, S1 = ▲, S2=■ , S3 = ● , S4 =◆ .